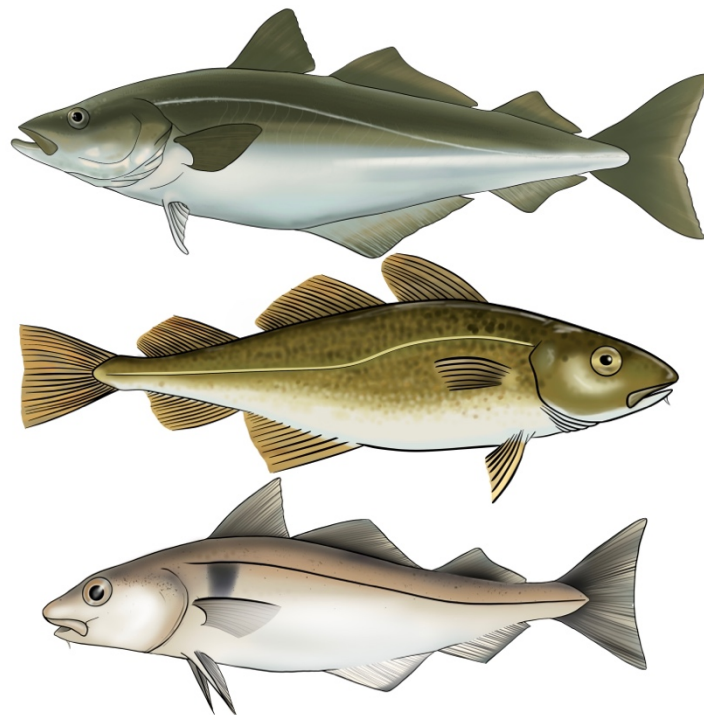


# A Comparative Study of the Spawning Phenology of Cod (*Gadus morhua*), Saithe (*Pollachius virens*), and Haddock (*Melanogrammus aeglefinus*): a Geographical Perspective along the Norwegian Coast



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## ABSTRACT

Reproductive traits are a fundamental aspect of an organism's life history and play a critical role in shaping population dynamics, as these traits can significantly influence offspring survival rates and, thereby, reproductive success. The timing and location of spawning events influence offspring survival rates and recruitment success in fish populations, marking them as crucial study areas for fisheries management and conservation. This master thesis aims to investigate the spawning phenology of three ecologically and commercially important fish species collected along the ocean areas surrounding Norway, from the North Sea to the Barents Sea: cod (*Gadus morhua*), saithe (*Pollachius virens*) and haddock (*Melanogrammus aeglefinus*), focusing on identifying potential differences in the timing and location of their spawning. I used a large dataset on gonadal development collected from scientific surveys and fishing vessels. The study area including the North Sea, the Norwegian Sea and the Barents Sea was divided into three regions: North, Mid and South. The research revealed several new spawning sites for all three species, not currently included in the official spawning maps used for management. Furthermore, I found variations in the timing of the spawning event both between and within the three species. In general, saithe appeared to reach peak spawning first, followed by cod and then haddock reaching the peak spawning last. Moreover, the peak spawning occurred significantly earlier in the southern area compared to the more northern areas for all species. The study also revealed variations in the duration of the spawning season, with cod and saithe having an overall shorter spawning duration than haddock. Identifying differences in the timing and location of the spawning event among these species' hints at unique adaptations to local environments. In summary, these findings provide important insights into the reproductive strategies of cod, saithe, and haddock from the North Sea to the Barents Sea. They further underscore the importance of research on the factors influencing the spawning.

Keywords: Cod, Haddock, Saithe, Spawning, Barents Sea, North Sea, Norwegian Sea

# TABLE OF CONTENT

<b>1 INTRODUCTION</b> .....	<b>1</b>
1.1 LIFE HISTORY TRAITS .....	1
1.2 THE SPAWNING EVENT AND REPRODUCTIVE TRAITS .....	1
1.3 RECRUITMENT VARIABILITY HYPOTHESES .....	2
1.4 RECRUITMENT AT HIGHER LATITUDES. ....	3
1.5 COD, SAITHE AND HADDOCK .....	5
1.6 AIM OF THE STUDY .....	6
<b>2 MATERIAL AND METHODS</b> .....	<b>7</b>
2.1 STUDY AREA AND SPECIES .....	7
<i>Study area</i> .....	7
<i>Study species</i> .....	9
2.2 DATA GATHERING .....	11
<i>Sampling platforms</i> .....	13
<i>Biological sampling</i> .....	15
2.3 DATA ANALYSIS .....	19
2.3.1 <i>Raw data</i> .....	19
2.3.2 <i>Statistical analysis</i> .....	20
2.3.6 <i>Extracting parameters to capture peak spawning</i> .....	23
2.3.7 <i>Area differences</i> .....	24
2.3.6 <i>Calculating the duration of the spawning season</i> .....	24
<b>3 RESULTS</b> .....	<b>25</b>
3.1 SPAWNING DISTRIBUTION .....	25
3.2 TEMPORAL DEVELOPMENT OF THE SPAWNING SEASON .....	27
3.3 PEAK OF THE SPAWNING SEASON .....	29
3.4 DURATION OF THE SPAWNING SEASON .....	34
<b>4 DISCUSSION</b> .....	<b>36</b>
4.1 SPAWNING DISTRIBUTION .....	36
4.2 PEAK OF THE SPAWNING SEASON .....	37
4.3 DURATION OF THE SPAWNING SEASON .....	39
4.4 LIMITATIONS .....	40
<b>5 CONCLUSIONS</b> .....	<b>42</b>
<b>REFERENCES</b> .....	<b>43</b>
<b>APPENDIX A</b> .....	<b>49</b>
<b>APPENDIX B</b> .....	<b>54</b>

# 1 INTRODUCTION

## 1.1 Life history traits

Life history theory refers to the study of how characteristics of one organism's life have evolved in response to ecological and environmental pressure. Numerous trade-offs have shaped these traits resulting from evolutionary forces acting over time (Stearns, 1992a). Studying life histories is important as it helps us understand the diversity of life strategies and anticipate how organisms may respond to future environmental changes (King & McFarlane, 2003). The life history traits differ among species, populations, and individuals (Jennings et al., 2001a), where different traits, and the combination of them, impact the fitness of an individual and its chance of survival and reproduction (Stearns, 1992b).

## 1.2 The spawning event and reproductive traits

In marine environments, there is a pronounced diversity of reproductive traits, which are the characteristics and patterns related to reproduction. The high variation of life histories is evident across various species and stocks (King & McFarlane, 2003). In marine fish species, particularly in teleost, we observe a variety of reproductive traits (Jennings et al., 2001a; Kawasaki, 1980), such as the number of eggs produced, the timing and location of spawning, the mode of reproduction, and offspring survival rate. One commonly observed trait among teleosts is their high fecundity, characterised by the production of thousands to millions of, often, pelagic eggs that can drift long distances before the hatched larvae develop the ability to swim and manoeuvre against the current (Jennings et al., 2001b)

Spawning is a central life history event shaped by a complex interplay of genetic, ecological, and behavioural factors. This complexity highlights the importance of investigating multiple life history traits and their interactions, particularly when studying recruitment variability. A better understanding of these relationships could enhance our capacity to predict and understand shifts in population dynamics, thereby improving the management of marine resources.

### 1.3 Recruitment variability hypotheses

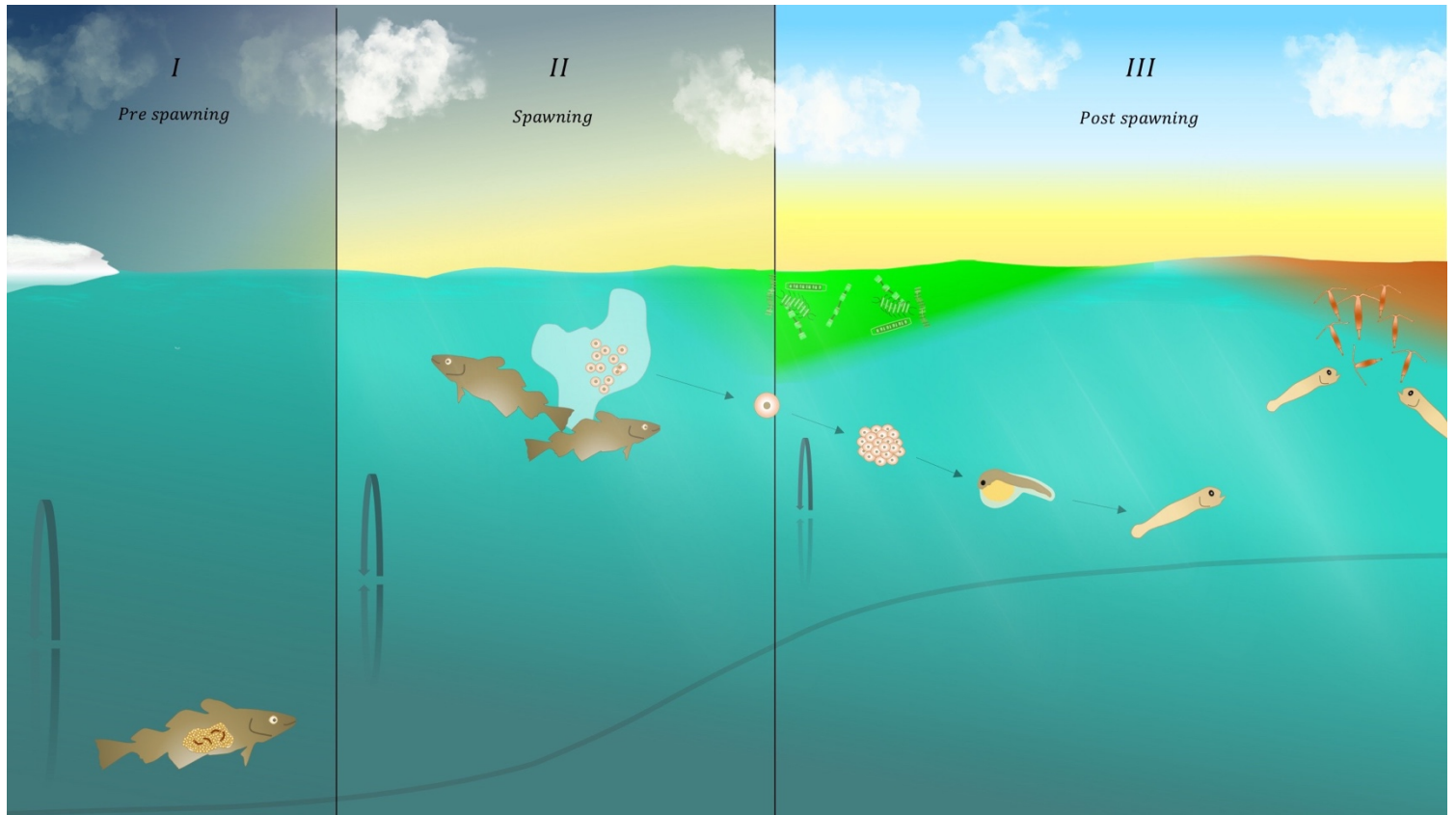
Through time, multiple scientific hypotheses have been proposed to explain the variability in stock recruitment, each aiming at identifying the factors that influence recruitment (Houde, 2016). One such hypothesis is the *critical period* hypothesis, proposed by Johan Hjort about a century ago (Hjort, 1914; Houde, 2016). Hjort suggested that the fate of a year class is primarily determined by the first-feeding larvae's ability to find sufficient food (Houde, 2016). The critical period commences when the yolk sac is absorbed, initiating a shift to external feeding for the larvae. During this period, the larvae's survival and growth are tied to food availability, a crucial phase that can impact the year-class strength (Hjort, 1914). Expanding on Hjort's ideas, Cushing (1990) linked the critical period to his *match-mismatch* hypothesis, which states that a match or a mismatch between the timing of the external feeding and the peak of the plankton bloom can significantly influence survival, as plankton is the main prey of fish larvae (Ferreira et al., 2020; Cushing, 1990). Mortality rates for larvae decline with body size (Houde, 1997), and, therefore, spawning should occur at a time that allows larvae to start feeding at the peak of their planktonic prey to enhance their survival (Cushing, 1990).

The offspring's survival depends not only on the spawning time but also on the event's location. The location of the spawning can impact how the ocean currents will distribute the larvae in time and space. The member-vagrant hypothesis, proposed by Iles & Sinclair (Iles & Sinclair, 1982; Sinclair & Iles, 1985) posits that recruitment success depends on the retention of eggs and larvae in favourable areas, which can vary from small-scale fjords to large-scale ocean basins (Houde, 2016). Spawning in specific areas enables the ocean currents to transport the eggs and larvae to locations that offer optimal feeding opportunities, thereby enhancing their growth and survival. Conversely, if the spawning occurs in less optimal areas, the transport mechanisms may lead the eggs and larvae to areas with insufficient food sources or unfavourable conditions, reducing their chances of survival.

#### 1.4 Recruitment at higher latitudes.

Most recruitment variability hypotheses are linked to the timing and extent of the spring bloom (Figure 1.1). Temperate and polar regions demonstrate distinct seasonal cycles in biological production (Jennings, 2001b; Sundby et al., 2016). These cycles commence with the spring bloom, an event characterized by a rapid increase in phytoplankton biomass. The increase in phytoplankton forms the foundation of the ocean food webs and initiates a cascade of productivity within the marine ecosystem (Jennings, 2001b). As the primary producers in marine ecosystems, phytoplankton convert solar energy into organic matter through photosynthesis, they form a fundamental food source for zooplankton and, in turn, creatures higher up in the food chain.

With increasing latitude, the duration of the spring bloom becomes shorter and more delayed but with a higher peak in the biomass (Racault et al., 2012; Siegel et al., 2002). Moreover, the spring bloom timing within a geographical area can display considerable yearly variations (Brander et al., 2001), which is influenced by several physical factors. The onset of the spring bloom is governed by a combination of factors where some remain stable across years, such as the solar elevation, while others, like weather patterns, can vary from year to year (Brander et al., 2001). The initiation of the spring bloom relies on the presence of sufficient light and mixing patterns, where a stratification in the upper part of the water column facilitates photosynthesis in phytoplankton and promotes their growth and reproduction (Figure 1.1) (Sverdrup, 1953; Mann & Lazier, 2006).



**Figure 1.1:** Simplified and schematic illustration of the spring bloom development alongside the spawning event. *I*) During the winter months, the stratification is low, leading to strong mixing of the water column, bringing nutrients from the ocean's deep up to the surface (Mann & Lazier, 2006). *II*) In the spring, the sun rises higher in the sky, along with increasing temperatures, heating up the ocean surface. The surface heating, combined with freshwater run-off, leads to increased water column stratification, where phytoplankton will be trapped in the upper water column, where sunlight is sufficient to start photosynthesis (Mann & Lazier, 2006). *III*) During the spring and summer, stratification will increase alongside the solar irradiation into the water column, leading to a rapid increase in photosynthetic organisms, indicating the onset of the spring bloom (Sverdrup, 1953). During this period, the zooplankton grazing on the phytoplankton will experience a rapid increase in biomass, which is the main prey of fish larvae (Mann & Lazier, 2006).

The ocean areas surrounding Norway cover vast geographical areas ranging from the North Sea (around 51 °N) to the Barents Sea (around 85.5 °N). The area is characterized by a wide range of temperatures and light conditions throughout the year (Sundby et al., 2016) and has large seasonal fluctuations in the peak of plankton biomass, both in timing and duration (Racault et al., 2012). The spawning event of many fish species on the North Atlantic Shelf seems to be linked to these seasonal cycles in plankton production, suggesting an evolutionary adaptation to strategically position their offspring in optimal feeding conditions (Brander et al., 2001).



## 1.5 Cod, saithe and haddock

Cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and saithe (*Pollachius virens*) are members of the Gadidae family and inhabit shelf ecosystems on both sides of the North Atlantic Ocean. These species form the basis for large fisheries in the ocean areas surrounding Norway and are important as prey and predators in the ecosystem they are a part of (Bergstad et al., 1987; Olsen et al., 2010).

Cod, haddock, and saithe share many similar life history traits. These species exhibit high fecundity batch spawning, a reproductive strategy where individuals can release multiple batches, each consisting of up to millions of eggs, within a single spawning season. Spawning typically occurs during the winter and spring when a large congregation of individuals come together in a confined space and time (Olsen et al., 2010). This reproductive strategy enhances the chances of some of the eggs and larvae to develop under optimal environmental conditions (Buckley et al., 2010), even considering the variable seasonal cycles in production from year to year in higher latitude areas (Racault et al., 2012). After spawning, their pelagic eggs, and larvae drift with the current as they develop to manoeuvre against the current.

Despite their many similarities, distinctions in recruitment variability are evident among cod, haddock, and saithe (Dolgov et al., 2013; ICES, 2020a; ICES, 2021). Saithe exhibit the most stable recruitment, followed by cod, while haddock exhibits the greatest fluctuations (Dolgov et al., 2013; ICES, 2021). These recruitment variations hint at differences in their life history and reproductive traits, significantly influencing their recruitment process. However, the specific reasons causing these differences are not fully understood (Johannesen et al., 2022).

Given that the spawning event is a critical stage for recruitment, the observed variations have a high probability of stemming from differences regarding the spawning event. As these species coexist in the oceanic regions around Norway, they likely have evolved distinct adaptations to minimize interspecific competition, to optimize resource use (Bergstad et al., 1987). These adaptations are likely also to include reproductive strategies, potentially causing differences in the spawning event and contributing to the variations in recruitment.

## 1.6 Aim of the study

The primary aim of this study was to investigate the spawning phenology of cod, haddock, and saithe along a latitudinal gradient spanning from the North Sea to the Barents Sea. A substantial dataset of gonadal development from fishery-independent and fishery-dependent sources have been utilized in this study. This dataset covers the years 2010 – 2021 and has never been used to investigate the spawning event of these three species.

More specifically, I will focus on the spawning phenology of cod, haddock, and saithe with the following objectives:

- (1) **Evaluate the current spawning maps used for management purposes against the data used in this study.** The objective is to compare existing spawning maps used for management purposes by the Institute of Marine Research (IMR) with the dataset used in this master thesis.
- (2) **Examine if there are any differences in the timing of the spawning events among cod, haddock, and saithe in different areas.** Given the coexistence of cod, saithe, and haddock and their shared life history and reproductive traits, it is plausible that these species have evolved strategies to mitigate interspecific competition. Consequently, I hypothesize that there will be variation in the timing of peak spawning among cod, haddock, and saithe across different oceanic locales surrounding Norway.
- (3) **Investigate the presence of a south-north gradient in the timing of the spawning peak for cod, haddock, and saithe.** Given the earlier onset of the spring bloom in lower latitudes, I anticipate that individuals in the south will spawn earlier than those in the north.
- (4) **Investigate the duration of the spawning season.** Given the shorter duration of the spring bloom in higher latitudes, I predict that the spawning individuals situated in the northern regions will exhibit a longer spawning duration compared to those in lower latitudes, to enhance the chance for at least some of the offspring to be spawned at an optimal time.

This master's thesis aims to provide new insight into the spawning event of these commercially and ecologically important species. By offering new insight into the spawning patterns of these three species, I hope to provide ideas for future research and essential information for improved decision-making concerning sustainable harvesting and marine conservation.

## **2 MATERIAL AND METHODS**

### **2.1 Study area and species**

#### **Study area**

The study area in this master thesis includes the North Sea, the Norwegian Sea, and the Barents Sea, along with the fjords and coastline, resulting in a comprehensive spatial coverage. Situated within the eastern North Atlantic Ocean, this region exhibits high variability in physical factors, including light conditions, temperature changes, and ocean currents throughout the year.

#### **The Barents Sea**

The northernmost part of the study area is the Barents Sea. The Barents Sea is located on the north coast of Norway, with boundaries stretching from the continental break in Northern Norway up to the west of the Spitsbergen archipelago. It stretches along the shelf break north towards the Franz Josef Land archipelagos and down towards the Kara Sea, covering about 1 600 000 km<sup>2</sup> (Ozhingin et al., 2011).

The Barents Sea is an ecosystem characterized by a shallow shelf with an average depth of 230 m (Smedsrud et al., 2013), ranging from 20 m at Spitsbergen Bank to 500 m in the Bear Island Trough. The area has several shallow, highly productive banks (Kędra et al., 2013) and different water masses influencing the ecosystem. The Barents Sea receives warm and saline water from the Atlantic Ocean in the southwest, while the Norwegian Coastal Current and the surrounding rivers provide an input of freshwater. These different water masses, along with the cold Arctic water from the Arctic Ocean in the north, contribute to the unique oceanography of the Barents Sea (Ozhingin et al., 2011). The interaction of these different water masses creates a dynamic boundary in the Barents Sea, known as a front system (Ozhingin et al., 2011), which impacts the distribution of marine organisms and their food sources (Titov & Orlova, 2011).

A remarkable feature of the Barents Sea is its extreme seasonal variation in sunlight. The sun does not rise above the horizon during winter, resulting in absolute darkness. Contrary, the sun remains above the horizon during the spring and summer, resulting in constant sunlight during day and night, a phenomenon known as the midnight sun. This results in a strong seasonal variation of primary production in the Barents Sea and plays a significant role in the marine life it supports (Titov & Orlova, 2011).

The Lofoten Islands are located to the south of the Barents Sea. While the surrounding shelf area of the Lofoten Islands falls within the boundaries of the Norwegian Sea, the area is an important spawning ground for several commercially important species that primarily inhabit the Barents Sea (Sundby et al., 2013). Hence, despite its geographical location within the Norwegian Sea, the Lofoten area is often included within the Barents Sea for management purposes (Ozhingin et al., 2011; Sundby et al., 2013)

### **The Norwegian Sea**

Moving southwards from the Barents Sea, we encounter the Norwegian Sea. The Norwegian Sea borders the Barents Sea in the northeast and the North Sea in the south, covering about 1 100 000 km<sup>2</sup>, and has an average depth of 1800 m, making it a relatively large and deep ecosystem (Skjoldal, 2004a). The Norwegian Sea is highly influenced by warm and saline Atlantic Water in the south, the cold Arctic Water from the northwest, and freshwater received from the Norwegian Coastal Current.

As for the Barents Sea, the high-latitude areas of the Norwegian Sea are exposed to strong seasonality in light, resulting in annual cycles in phytoplankton production and growth of both fish and zooplankton (Skjoldal et al., 2004b).

### **The North Sea**

The southernmost sea around Norway is the North Sea, stretching northwards from the English Channel at 51 °N and covering a vast area of approximately 570,000 km<sup>2</sup>, with a border at 62 °N towards Shetland (Probs et al., 2021). The North Sea is a large continental shelf with several shallow banks (Hestetun et al., 2018). This shallow marine ecosystem has an average depth of 90 m, deepening towards the north around the Norwegian Sea and the Norwegian Trench that follows the southwest tip of Norway (Hestetun et al., 2018). The area is highly influenced by the inflow of warm and saline water from the Atlantic Ocean into the northern North Sea and low-salinity water from the Baltic Sea and the rivers surrounding the North Sea.

An important part of the Barents Sea, the Norwegian Sea and the North Sea are their coastal areas. Shallow depths, banks and fjord systems characterize these coastal areas. The fjords along the Norwegian coastline are crucial marine ecosystems, providing habitats for diverse marine organisms (Hestetun et al., 2018). The fjords can exhibit different characteristics, ranging from open systems with significant water exchange with the oceanic water outside the

fjord to more closed systems, often featuring a shallow sill that restricts water exchange (Aksnes et al., 1989). In more closed fjord systems, we often find more isolated populations of marine organisms, as individuals are less likely to get advected out of the fjord (Hestetun et al., 2018).

## Study species

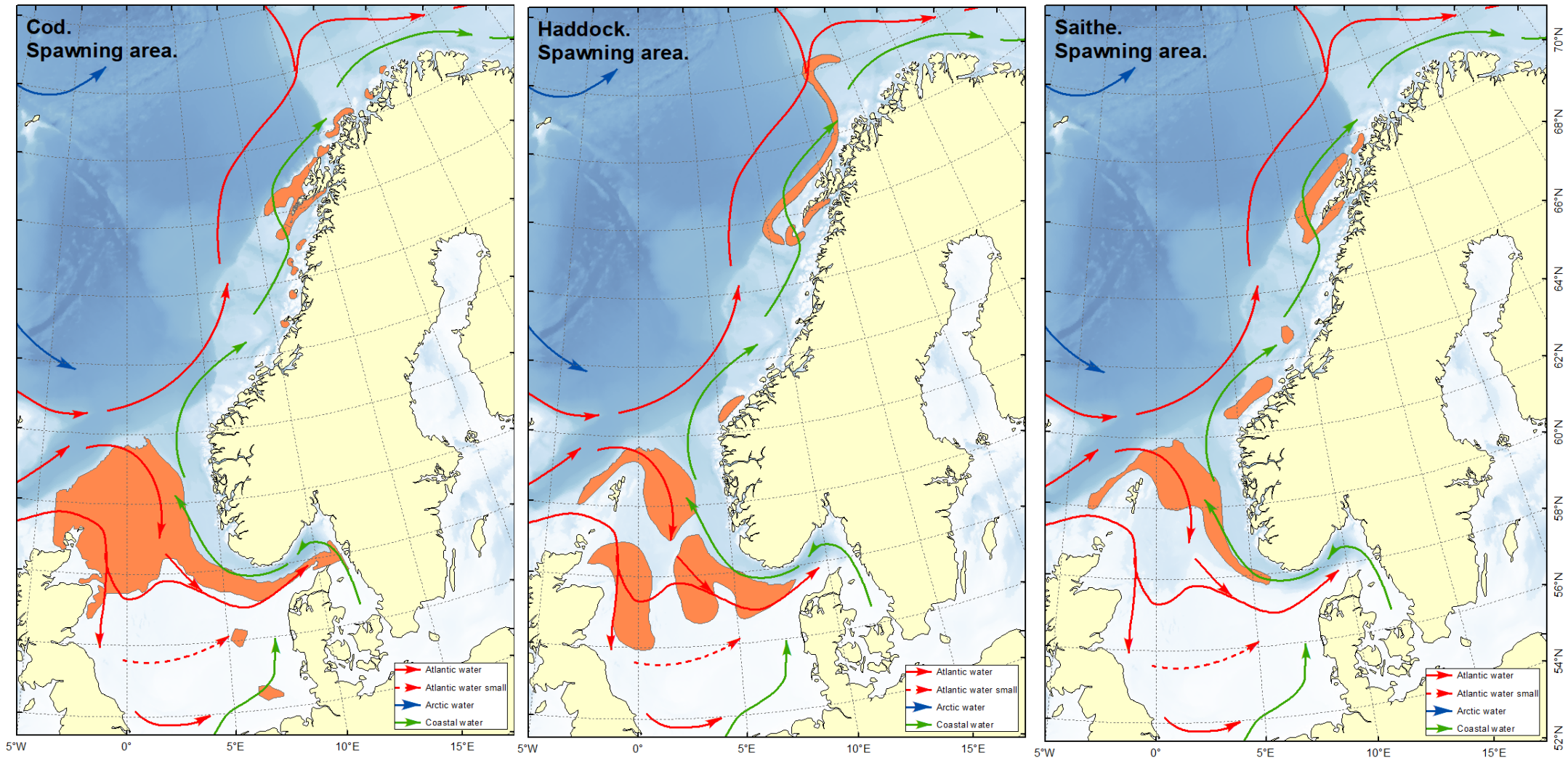
The study species in this master thesis are the cod, saithe, and haddock, which inhabit the shelf ecosystem on both sides of the North Atlantic Ocean. These species are highly abundant in the designated study area, where they play a vital role in the marine ecosystem and commercial fisheries (Bergstad et al., 1987; Olsen et al., 2010).

Due to the high abundance and wide distribution of cod, haddock and saithe within this geographical area, management has established geographical boundaries to identify and manage these different stocks. This approach is maintained even in light of the potential migration across these borders. Establishing management boundaries often requires a trade-off between the actual population structure and the scale of available monitoring data. For management purposes cod, haddock, and saithe are divided into two main stocks: The North Sea stocks found south of 62 °N and the Northeast Arctic stocks found north of 62 °N.

Cod has been the primary focus of research in this region, resulting in the identification of several stocks and sub-populations. Along the Norwegian coastline, cod are divided into three stocks based on these geographical management boundaries: coastal cod south of 62 °N, coastal cod between 62 °N and 67 °N, and Coastal cod north of 67 °N. Differentiating between coastal cod and Northeast Arctic cod north of 62 °N demands careful analysis of morphological features in otoliths (Stransky et al., 2008) or through genetic sampling (Dahle et al., 2018a).

Recent studies have also revealed distinct sub-populations within the North Sea cod stock (ICES, 2023). Until now, the North Sea cod has been managed as a single stock, but in light of the new findings, new management strategies are now under development (ICES, 2023).

Spawning maps are important tools used in management and are frequently updated when new information and insights are gained through research and monitoring activities (Sivle & Johnsen, 2016) (Figure 2.1). Several spawning locations for these three species are found in this study area, along the continental shelf and coastal areas and fjords. These spawning maps can provide important insight into the population structure of these ecologically and commercially important species. Consequently, they can enhance decision-making processes related to management strategies and regulate human activity in the areas (Sundby et al., 2013).



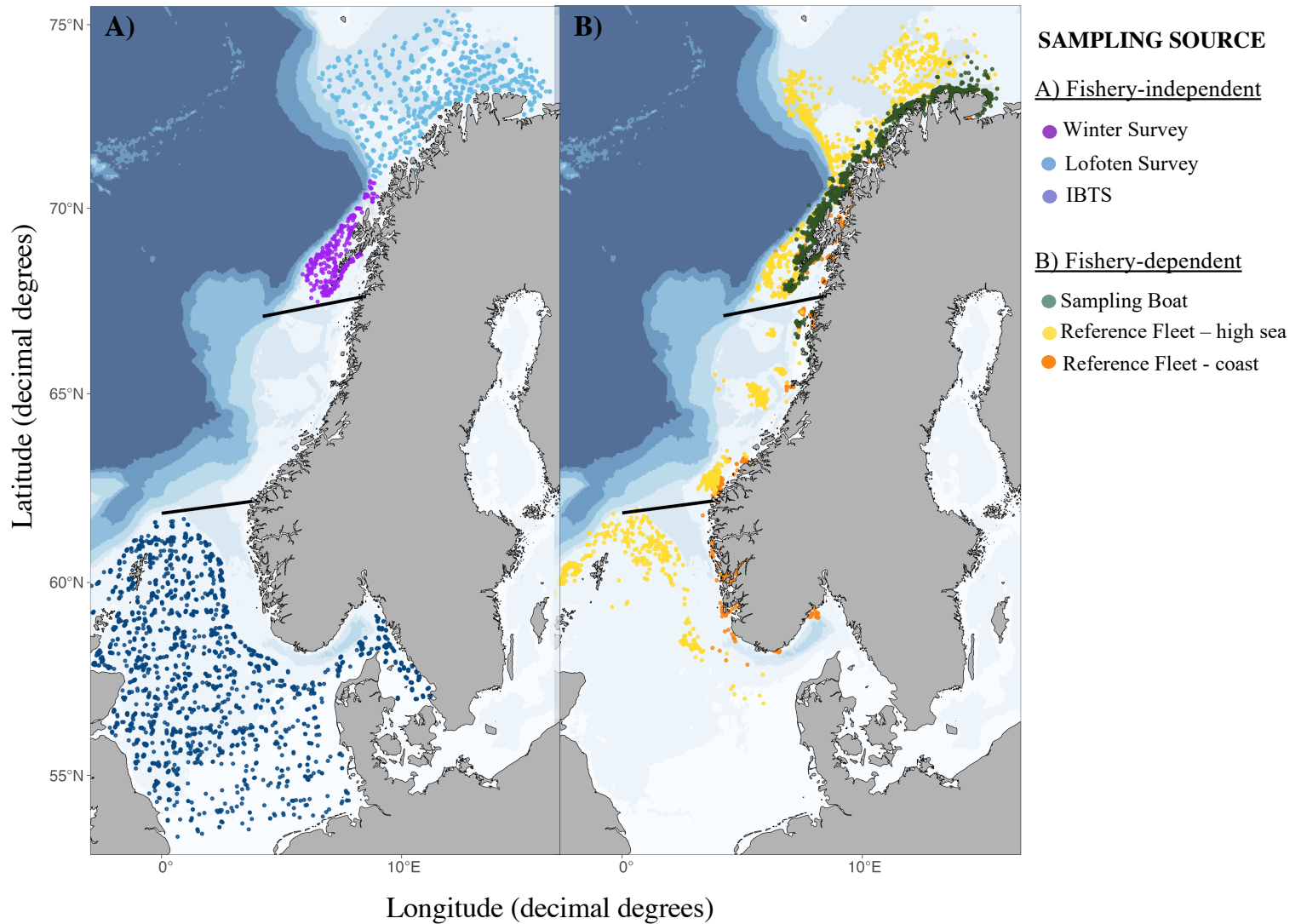
**Figure 2.1:** Identified spawning areas (highlighted in orange) for cod, haddock, and saithe along the Norwegian coast. The arrows on the map indicate the ocean currents in the area, with colours representing the transported water masses: red solid = Atlantic Water, red dashed = Atlantic Water small, blue = Arctic Water, and green = Coastal Water. Kjell Bakkeplass compiled this map in February 2023.

## 2.2 Data gathering

Data from various sampling platforms (Figure 2.2), each with its unique data collecting methods and objectives, collected between January to June in the years 2010 to 2021 (Appendix A.1) have been utilized to investigate the spawning phenology of cod, haddock, and saithe.

The Institute of Marine Research (IMR) is responsible for several fishery-independent surveys, where data are collected using standardized methods. These surveys include the Barents Sea NOR-RUS demersal fish cruise in winter (hereafter referred to as the Winter Survey) and the Lofoten NOR demersal fish cruise in Mar\_Apr (hereafter referred to as the Lofoten Survey). The IMR also manages the Sampling Boat and the Norwegian Reference Fleet. These sample platforms provide fishery-dependent data, where scientific samples are taken directly from commercial catches. The International Council for Exploration of the Sea (ICES) conducts the International Bottom Trawl Survey (hereafter referred to as IBTS), a fishery-independent data source.

The geographical focus of this study includes the North Sea, the Norwegian Sea and the Barents Sea. Using the statistical areas defined by the Norwegian Directorate of Fisheries (DFO), we have divided these areas into three specific regions (Appendix A.2). These regions are based on their geographical locations in relation to 62°N and 67°N. The three defined regions are the South area (south of 62°N), the Mid area (62°N to 67°N) and the North area (67°N and northwards).



**Figure 2.2:** Overview of the study area and sampling locations for fishery-independent and fishery-dependent data. A) The left map displays the location where fishery-independent data was collected during the Winter Survey, Lofoten Survey and IBTS. B) The right map shows the location where fishery-dependent data was collected from the Sampling Boat, the Reference Fleet - high seas and the Reference Fleet - coast. The locations are marked with dots, where their colours indicate the specific data source. Only stations with the recorded presence of female cod, haddock and saithe noted with maturation stages 2, 3 and 4 collected from 2010 – 2021 are represented.



## Sampling platforms

Although the data collection methods used across various sampling platforms were not initially designed to address this master's thesis research questions, the combination of these data sources provides a comprehensive dataset that can enhance the understanding and answers to the objectives of this thesis. The following section will provide an overview of these data sources.

### **IBTS**

The International Council for the Exploration of the Sea (ICES) coordinates the International Bottom Trawl Survey (IBTS). This survey aims to establish independent indices of fish distribution and relative abundance of mainly demersal species in the North Sea using a bottom trawl (ICES, 2020b). This survey is a collaboration between Norway, Denmark, France, Germany, the Netherlands, the UK, and Sweden.

### **Winter Survey**

The winter survey investigates the abundance and distribution of demersal fish stocks in the Barents Sea using a bottom trawl (Fall et al, 2020). The survey has been a collaboration between the Institute of Marine Research (IMR) and the Russian Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO). The survey starts in January, where several research vessels cover the ice-free zone in the Barents Sea, from the Spitsbergen Archipelago to the south part of Novaya Zemlya, continuing southwards towards Tromsø where it ends in March.

### **Lofoten Survey**

Lofoten Survey is an acoustic survey that monitors Northeast Arctic cod's spawning stock and spawning grounds (Fuglebakk & Thorsen, 2022). The survey covers the coastal areas from 70°N southwards toward Røstbanken and Vestfjorden, located inside of Lofoten Island, from March to April. During the Lofoten Survey, acoustic data combined with egg samples and fish samples have been collected (Fuglebakk & Thorsen, 2022), where only the latter is included in the dataset in this thesis.

### **The Norwegian Reference Fleet**

The Norwegian Reference Fleet is a group of active fishing vessels that provide fishery-dependent information about catches and fishing activity to the Institute of Marine Research (IMR) (Clegg & Williams, 2020). The Norwegian Reference Fleet is divided into two groups: the Coastal Reference Fleet, covering the areas along the Norwegian coast, and the high-seas Reference Fleet, covering the ocean areas off the Norwegian coast.

IMR selects these vessels based on their targeted species, spatial and temporal coverage, as well as the fishing gear used, enabling extensive coverage of fish abundance and distribution in time and space along the Norwegian coast and the ocean areas off the Norwegian coast. These fishing vessels have the same measuring instruments as those on IMR research vessels. The selection of which hauls the scientific samples are conducted varies depending on the fishing gear used (Clegg & Williams, 2020).

### **Sampling Boat**

The sampling Boat is a fishery-dependent source of information, providing IMR with information about the commercial fisheries and their landing. Through the Sampling Boat, the IMR staff takes scientific samples of the landings from commercial fishing vessels (Havforskningsinstituttet, 2021). A rented vessel covers northern Norway between Varangerfjorden and Helgeland, travelling between different landing sites.

The IMR staff selects fishing vessels from which biological samples are taken. These selections are based on the vessel's fishing location and the gear used to get extensive coverage of different species caught with different tools and at various sites. Samples are primarily collected from boat fishing close to the coast, as the fishing vessels in the high seas tend to freeze the fish, making it hard to take biological samples.

## Biological sampling

This thesis focuses on a dataset that includes individuals with documented maturation stages. Each individual in this dataset has been subjected to detailed biological sampling, where their length, weight, age, sex and maturity stage have been recorded. Although length measurements are typically conducted on all individuals, other detailed measurements, such as the noted maturation stage, are only performed on a selected number of individuals. The protocol for measurements varies across these different sampling platforms, where either a selected number from the total catch or a predetermined number of individuals within different length groups are selected for detailed measurements (Table 2.1)

**Table 2.1:** Overview of the biological sampling procedure for cod, haddock, and saithe across different sampling platforms. These procedures are specific to each haul where scientific sampling takes place. The table shows the number or the selection process of individuals from whom the maturation stage is determined, alongside other detailed scientific samples.

<b>SAMPLING PLATFORM</b> (time sampled <sup>1</sup> )	<b>COD</b>	<b>HADDOCK</b>	<b>SAITHE</b>
<b>Winter Survey</b> (Jan – Mar, 2010 – 2021)	Individuals > 20 cm: First individual for every 5 cm length group	Individuals > 20 cm: First individual for every 5 cm length group	None
<b>Lofoten Survey</b> (Mar – Apr, 2010 – 2021)	Five first individuals for every 5 cm length group  Hauls containing large catches of cod: The ten first individuals for every 5 cm length group	Five first individuals for every 5 cm length group	Five first individuals for every 5 cm length group
<b>IBTS</b> (Jan – Mar, 2010 - 2021)	First individual for every 1 cm length group	Individuals 11 – 30 cm: The two first individuals for every 5 cm length group  Individuals > 30 cm: The two first individuals for every 1 cm length group	First individual for every 1 cm length group
<b>The Norwegian Reference Fleet</b> (Jan – May, 2011 – 2021)	Twenty samples of each species are taken <sup>2</sup>	Twenty samples of each species are taken <sup>2</sup>	Twenty samples of each species are taken <sup>2</sup>
<b>Sampling Boat</b> (Jan – Jun, 2011 – 2021)	Twenty samples are taken in total, where sex and maturation are determined if possible	Twenty samples are taken in total, where sex and maturation are determined if possible	Twenty samples are taken in total, where sex and maturation are determined if possible

<sup>1</sup>The study utilises data collected from January to June (2010 – 2021). Any data gathered outside January to June, even though available, have not been incorporated in the dataset.

<sup>2</sup>In theory, the maturation stage is only determined until the 1st of May – but samples after this date, until June, have been used in the statistical analysis.

**Maturation scale**

The maturity scales utilized for cod, haddock and saithe display differences between the IMR-related sampling platforms and the IBTS survey (Table 2.1) (Mjanger et al., 2010; ICES, 2018). Over the past 11 years, the IBTS survey has incorporated two distinct maturation scales (M6 and SMSF), in contrast to the IMR-associated surveys, which have consistently used one single maturation scale. To standardize the data from these two maturity scales, the IBTS's maturity scales have been translated to align with the single scale utilized by IMR (Table. 2.2).

In this study, only maturation stages 2, 3 and 4 will be used further in the data exploration and statistical analysis. These stages indicate that the individuals are mature and capable of spawning.

**Table 2.2:** Overview of the maturation scales used by IMR (Winter Survey, Lofoten Survey, the Norwegian Reference Fleet, and the Sampling Boat) and IBTS surveys, describing the meaning of the different stages. The dark grey area shows this paper's translated maturation stages with the red-coloured maturation stages (2, 3 and 4) used in this thesis.

IMR	IBTS		DESCRIPTION	COMBINED
	M6	SMSF		
<b>1</b>	<b>61</b>	<b>A</b>	<b>Immature</b>	1
		<b>B</b>	<b>Developing</b>	
<b>2</b>	<b>62</b>	Ba	Developing but functionally immature	<b>2</b>
		Bb	Developing and functionally mature	
		<b>C</b>	<b>Spawning</b>	
<b>3</b>	<b>63</b>	Ca	Actively spawning	<b>3</b>
		Cb	Spawning capable	
		<b>D</b>	<b>Regenerating</b>	
<b>4</b>	<b>64</b>	Da	Regressing	<b>4</b>
		Db	Regenerating	
	<b>65</b>	<b>E</b>	<b>Omitted spawning</b>	
<b>5</b>	<b>66</b>	<b>F</b>	<b>Abnormal</b>	5

## 2.3 Data analysis

### 2.3.1 Raw data

Data on cod, saithe and haddock containing maturation stages were retrieved from the IMR and ICES databases and imported into R. The raw data included information about the sampling time, geographical position, name of the sampling platform, the boat used, species, weight, length, sex, maturation stage and age for each individual. The raw data were checked for outliers, but no modification was necessary.

To prepare the raw data for analysis, the statistical areas from the Norwegian Directorate of Fisheries and the day number of capture were added to the dataset, and the maturation stages were transformed. The statistical areas were used to divide the sampling area into three zones: South, Mid and North (Appendix A.2). The term “day number” refers to as the number of days since January 1<sup>st</sup> until the day of capture.

It is worth noting that the Norwegian Reference Fleet contributed to a substantial portion of the data related to this study (Appendix A.3). Even though their sampling of the maturation stages officially ends on day 120, I have included any available data beyond this date, as this allows for a comprehensive coverage of the spawning season of all three species. To maintain transparency, day 120 – the official ending of the maturation stage sampling for the Norwegian Reference Fleet – will be consistently marked in the graphical presentations in the result section.

### 2.3.2 Statistical analysis

The aim of the statistical analysis was to investigate the spawning phenology of cod, haddock, and saithe along the Norwegian coast and identify potential geographical differences in the spawning event. The analyses focused on mature female individuals sampled between January and June (2010 – 2021), specifically those classified with maturation stages 2, 3 or 4. Immature individuals (maturation stage 1) and uncertain individuals (maturation stage 5) were excluded from the dataset.

Maturation stages 2 and 4 indicate that individuals were either in the process of developing their gonads to spawn or had already spawned or skipped spawning, meaning they were sexually mature but not actively spawning at the time of sampling, while maturation stage 3 indicated a spawning individual. Before the analysis, all remaining individuals were coded as either 1 (spawning individual, maturation stage 3) or 0 (non-spawning, sexually mature individual, maturation stage 2 or 4), creating a binary response variable. In total, 105 868 individuals were used in the statistical analysis, cod: 53 279, haddock: 34 388 and saithe: 18 201 (Table 2.3).

The data cleaning, statistical analyses and visualization were done in R (v. 4.2.2) (for specific R packages used, see Appendix A.4).

**Table 2.3:** Number of individuals of cod, haddock and saithe used in the statistical analysis, divided by area and spawning status (1 = spawning individual, maturation stage 3, 0 = non-spawning, but mature individual, maturation stage 2 or 4).

SPAWNING / NOT SPAWNING	COD			HADDOCK			SAITHE		
	North	Mid	South	North	Mid	South	North	Mid	South
<b>1</b>	10 158	935	865	2 885	985	4 816	1 293	2 381	1 639
<b>0</b>	34 569	2 213	4 539	11 699	2 385	11 618	5 566	3 255	4 067
<b>Total</b>	<b>53 279</b>			<b>34 388</b>			<b>18 201</b>		



## Probability of being a spawner

The statistical analysis aimed to observe the probability of cod, haddock, or saithe to be a spawner on given days throughout the spawning season across three different areas: South, Mid, and North. The concept of “Day number” represented the count of days since January 1<sup>st</sup> and was used as a predictor of the probability of being a spawner.

For spring spawners, the probability of a mature individual to be a spawner is assumed to first increase from the onset of the spawning season, typically in late winter or early spring. This probability is presumed to reach a maximum at the time when most individuals are spawning before the probability decline as the spawning season ends in late spring/ early summer.

An exploratory analysis with Generalized Additive Model (GAM) was done to investigate the relationship between the binary response variable (spawning 1 / not spawning 0) and the predictor variable (day number) The GAM can model highly complex non-linear relationships, as it does not assume a specific shape of the relationship between the predictors and the response. A GAM can therefore be used to explore how the probability of an individual being a spawner will change during the spawning season, at the different areas.

To predict the occurrence of a binary outcome – in this case, the probability of an individual being a spawner at different times and different locations – I employed a logistic regression. This is a form of generalized linear model (GLM), with binomial distribution and a logit link function. This logit link function (Eq. 2.1) is applied to model the probability of success (in this case, an individual spawning (1)) as a function of the independent variables (the day number and the area). Using the logit link, we can eliminate the upper and lower boundaries of the probability from 0 to 1, so that the response can range from negative to positive infinity.

$$\text{logit } p(s) = \log \frac{p(m)}{1 - p(m)} = \beta_0 + \beta X \quad (\text{Eq. 2.1})$$

$\beta_0$  is the intercept,  $\beta$  is the coefficients of the predictor  $t \beta_1, \dots, \beta_i$  for a corresponding set of predictors ( $x_1, \dots, x_n$ ) noted as  $X$ . The binary response is represented by  $s$ .

To predict the results as probabilities, we take the inverse of the logit link function and back-transfer the response from the logit scale to probabilities ( $p$ ) ranging from 0 to 1 (Eq.2.2).

$$p(s) = \frac{e^{\beta_0 + \beta X}}{1 + e^{\beta_0 + \beta X}} \quad (Eq. 2.2)$$

The Generalized Linear model (GLM) assumes an underlying linear relationship between the predictor and the response. To allow a bell-shaped relationship between the predictor and response, a quadratic term (Eq. 2.3) was included into the GLM.

$$\text{logit } p(s) = \beta_0 + \beta_1 t_1 + \beta_2 t^2 \quad (Eq. 2.3)$$

With  $t$  being the time since January 1<sup>st</sup>.

### **The model parameters for the full model**

To investigate the factors influencing spawning, a GLM was fitted with the binary response variable, spawning (1 / 0) and the predictor variables “day of year” and day of the year as a quadratic term and “area”.

Given the objective to investigate the presence of a geographical gradient in the timing of the spawning events, an interaction term was included between “day number” and day of the year as a quadratic term and “area”.

### **The full model was then:**

spawning ~ daynumber + daynumber : area + daynumber<sup>2</sup> + daynumber<sup>2</sup> : area + area,  
family = binomial, link = logit

Which, implicitly, allows for area-specific coefficient  $\beta_0$ ,  $\beta_1$  and  $\beta_2$  in equation 2.3:

$$\text{logit } p(s) = \beta_{0,a} + \beta_{1,a} t_1 + \beta_{2,a} t^2$$

The full model was fitted to each species separately and compared to simpler models using the Akaike Information Criterion (AIC) (Appendix A.6).

### 2.3.6 Extracting parameters to capture peak spawning

Using a logistic regression model with a quadratic term (GLM model), the fitted values follow a parabolic shape on the logit scale. This shape provides valuable information for identifying the day number with the highest probability of observing a spawning individual throughout the spawning season, accounting for different areas and species. However, this method does not directly provide information about the uncertainty of the estimated value.

The delta method is a statistical technique that estimates the distribution of a function of random variables. It allows for the estimation of specific values, as well as their standard error and their confidence interval. The delta method can therefore be used to locate the time with the highest probability of observing a spawning individual, also with uncertainty.

To identify the time with the highest probability of observing a spawning individual with the delta method, we need to find the maximum point of the function. To do this, we need to find the derivative of the function with respect to  $x$  and set it equal to zero as this marks the point from where the slopes transition from increasing to decreasing.

By setting the derivative of equation 2.3 to zero, and solving it, we can determine the day number that corresponds to the peak of the parabolic curve, representing the day number with the highest probability of observing a spawning individual using delta method (Eq. 2.4).

$$t = \frac{-\beta_1}{2\beta_2} \quad (\text{Eq. 2.4})$$

Where  $\beta_1$  and  $\beta_2$  can be coefficients specific to an area, depending on the best model selected (see previous section about model selection).

### 2.3.7 Area differences

In the case when area specific coefficients are relevant, one can estimate the differences between the two estimated peaks with uncertainties (Eq. 2.5).

$$\left(\frac{-\beta_{1a}}{2\beta_{2a}}\right) - \left(\frac{-\beta_{1b}}{2\beta_{2b}}\right) \quad (\text{Eq. 2.5})$$

Where  $\beta_{1a/b}$  and  $\beta_{2a/b}$  are coefficients specific to the areas compared.

### 2.3.6 Calculating the duration of the spawning season

To estimate the duration of the spawning season, I utilized the predicted values obtained from the Generalized Linear Model (GLM). This process involved identifying the peak of the probability curve and determining the day at which the probability value representing half of the maximum probability of being a spawner occurred. The duration of the spawning season was calculated as the number of days between these two points.

## 3 RESULTS

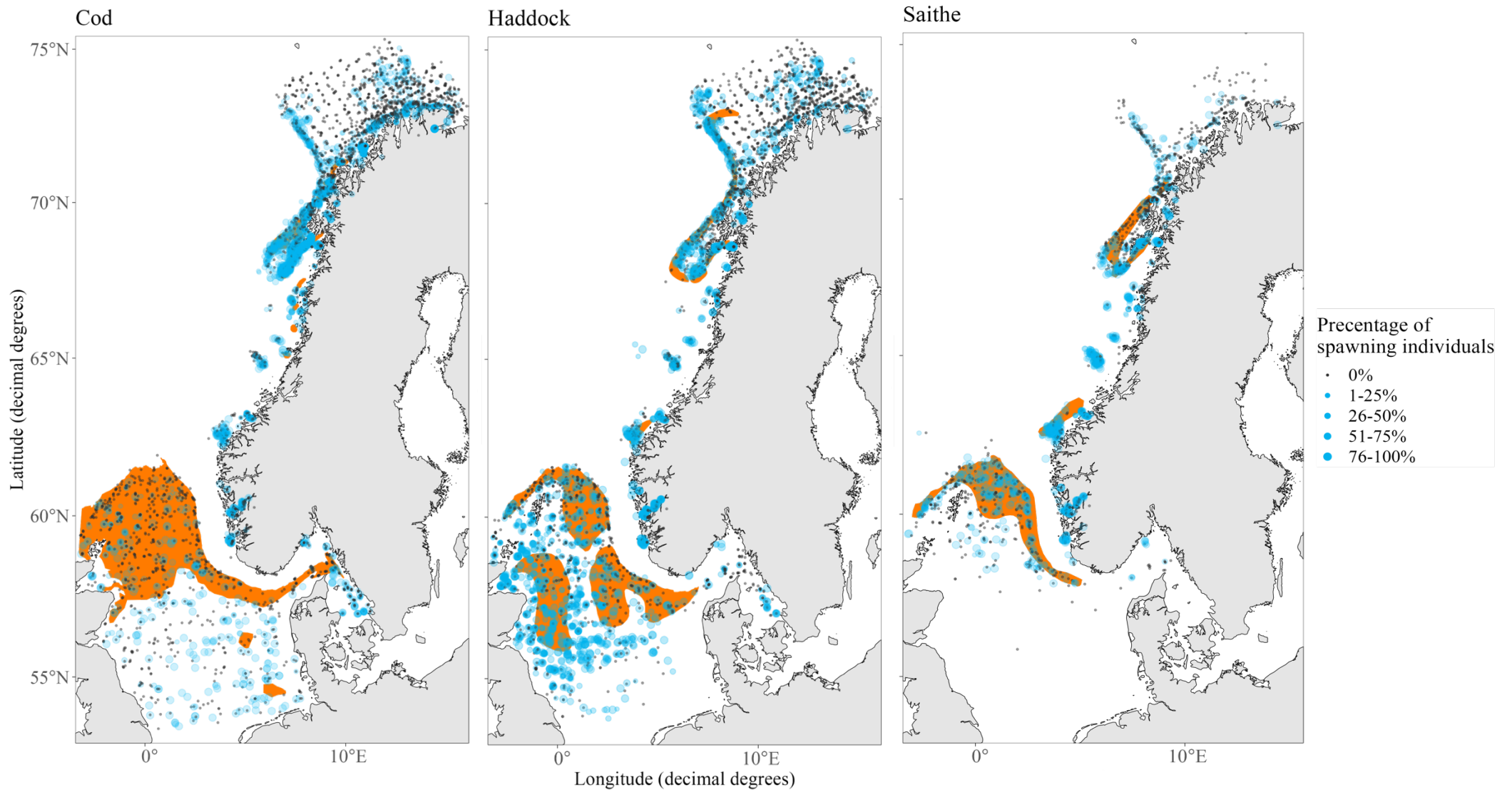
### 3.1 Spawning distribution

The maps presented in this thesis (Figure 3.1) reveal a more extended northeast spawning distribution of cod, haddock and saithe than currently documented on existing spawning maps. Specifically, data demonstrate a spawning area for these species in the Tromsøflaket region (Appendix B.1) and along the coast of northern Norway. Existing spawning maps only represent this distribution for haddock and minor spawning sites for cod located along the coast north of Lofoten. Additionally, cod and haddock exhibit spawning activity towards the North Cape Bank (Nordkappbanken, Appendix B.1), northeast of Tromsøflaket.

Shifting the attention southwards, several smaller spawning locations for all species are found along the coastline, spanning from the Lofoten area to the southernmost tip of Norway. Many of these spawning areas seem to be spawning grounds for all three species, where several of these are not described in the existing spawning maps.

In the southern part of the study area, in the North Sea, distinct aggregations of spawning haddock and saithe are observed in the north area. The spawning of these two species aligns well with the current spawning maps. However, the current maps seem to lack the haddock's spawning regions in the southeast and mid areas of the North Sea.

The distribution of spawning cod appears to be evenly spread across the North Sea, contradicting the current spawning maps that suggest a concentration of spawning grounds in the northern North Sea and where they have a spawning distribution spanning along the Norwegian Trench.



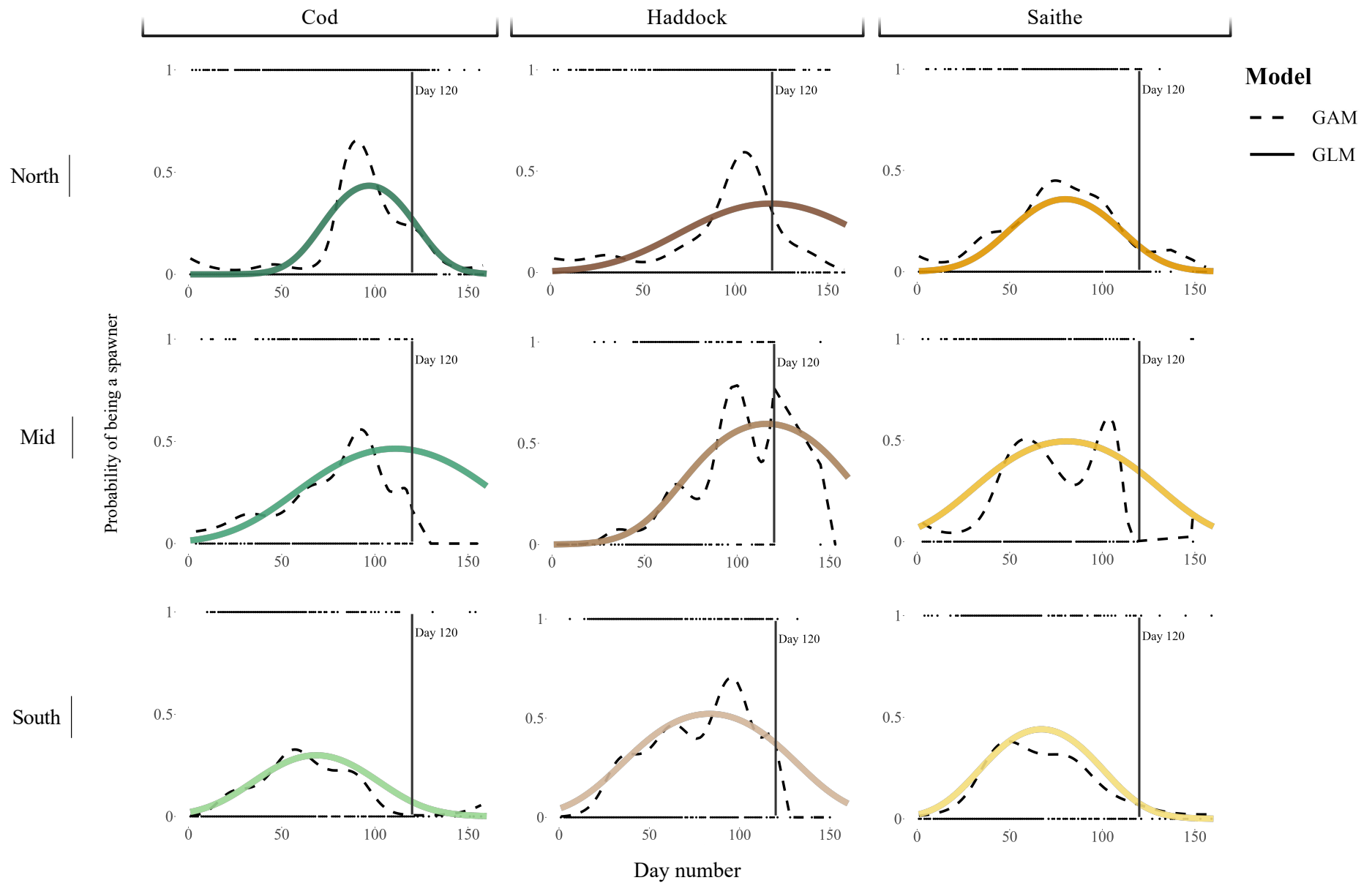
**Figure 3.1:** Spawning distribution maps of cod, haddock, and saithe along the Norwegian coast (orange areas, which are the known spawning areas), overlaid with sampling stations where individuals with maturation stages 2, 3 and 4 were captured, marked as points. The size and colour of the points at each station indicate the percentage of spawning individuals during the sampling (maturation stage 3), against the total number of individuals sampled at each station (maturation stages 2, 3 and 4). Black dots indicate stations where no stage 3 individuals were sampled, while blue dots represent stations where at least one stage 3 individual where sampled. The proportion of stage 3 individuals was divided into five categories: 0%, 1-25%, 26-50%, 51-75%, and 76-100%, with the size of the dots representing the percentage.

### 3.2 Temporal development of the spawning season

The shape of the predicted values from the GAM and GLM seems to align to some degree for all areas and all species (Figure 3.2). However, the two models were more similar in the southern area compared to the northern area for all species. Moreover, saithe seems to demonstrate a higher degree of similarity between the peak spawning in the GAM and GLM across all regions when compared to cod and haddock.

The probability of being a spawning individual in the southern region showed a more gradual increase, spawning over a longer time for all species, in contrast to the Mid and North area, where a steeper incline in the probability of being a spawning individual was detected with the GAM, especially for cod and haddock.

The GAM exhibited a more marked increase and decrease than the GLM, hinting at a more distinct peak. Despite this, there was a high similarity between the two models overall. I therefore, proceeded analyzing the results from the full GLM.



**Figure 3.2:** The probability of being a spawner as a function of day number and area predicted from the full model, a GLM (solid line) and a GAM (dashed line), with both models explicitly run for each species. The maturity stage is marked as 0 for mature but non-spawning individuals and 1 for spawning individuals. Day number 120 marks the end of the maturation stage sampling period for the Reference Fleet, a significant data source in this dataset. Some data collection continued beyond day 120, but the number of samples collected post this day was limited.



### 3.3 Peak of the spawning season

The fitted values from the full GLM model were used to investigate the peak timing of the spawning season for cod, haddock, and saithe across different areas (Fig. 3.3; Table.3.1). The results indicated that there was a difference in the timing and peak of the spawning season between species, but also between areas.

#### **Differences between species**

The timing of the peak of the spawning season differs between cod, haddock, and saithe in the different areas (Figure 3.3; Table 3.1). In the South area, cod reached their spawning peak earlier than saithe and haddock, while in the mid and northern regions, saithe was the first to reach peak spawning, followed by cod and then haddock.

There seems to be a consistent number of days between the spawning peaks for the species at the different areas. There is one exception for cod and saithe in the southern region, where the number of days differing the speak spawning was only two days. The number of days between the different peaks ranged from 16 to 36 days. Specifically, in the southern region, the time between the peak of saithe and haddock was approximately 20 days. In the mid-region, saithe and cod had a 24-day difference, and cod and haddock had a 17-day difference. In the northern region, there was a 23-day difference between cod and saithe, and a 36-day difference between cod and haddock.

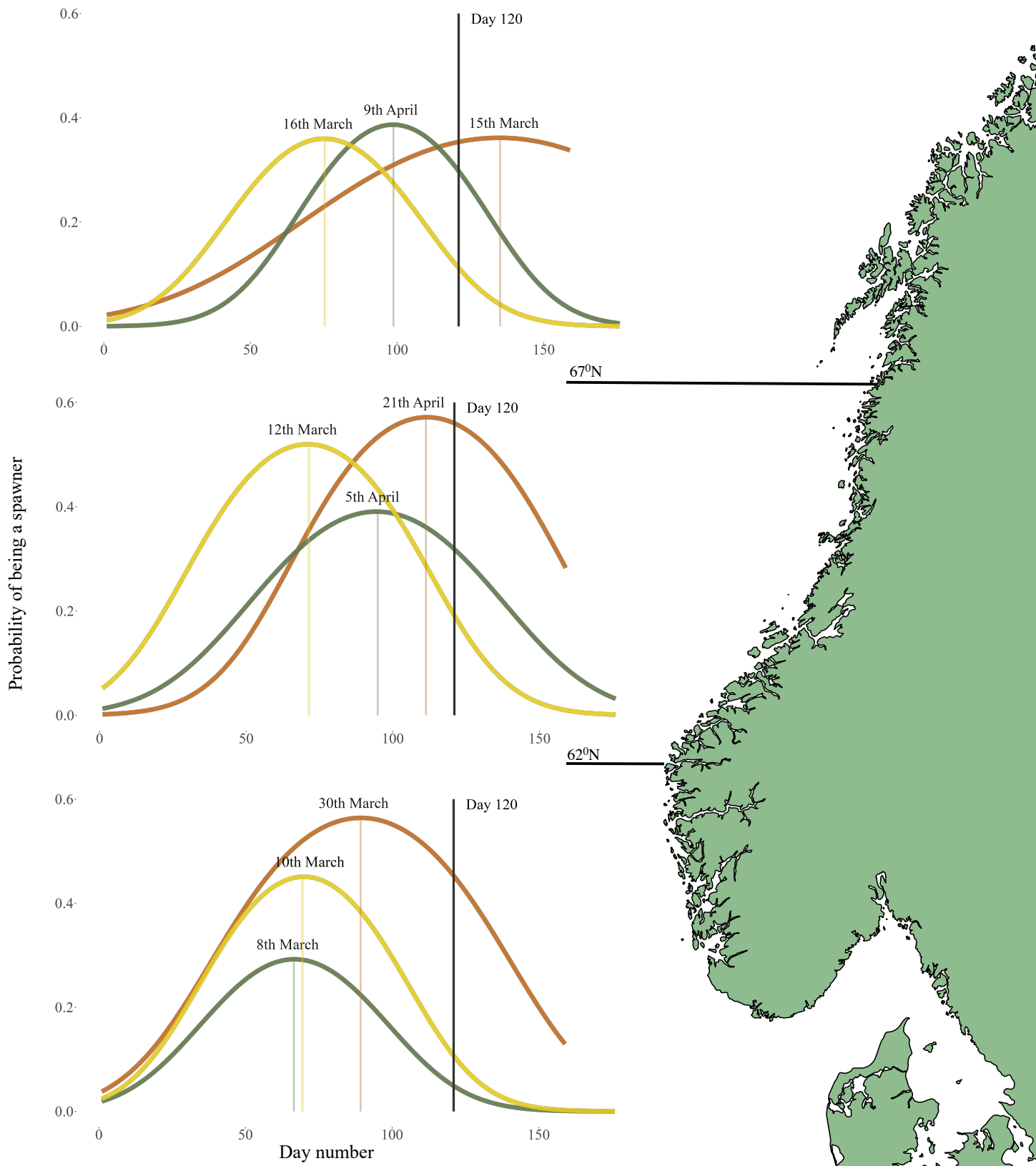
#### **Differences between areas**

There was a difference in the timing of the spawning peak along a south-north gradient for all species (Figure 3.3). All species had the earliest peak in the south area (from 8<sup>th</sup> of March to the 30<sup>th</sup> of March), followed by a later peak in the mid (from 12<sup>th</sup> of March to 22<sup>nd</sup> of April), and the latest peak in the northern area (from 16<sup>th</sup> of March to 15<sup>th</sup> of May).

The differences in the peak of the spawning season were relatively small for saithe, with only a couple of days difference from south to mid (2 days), and mid to north (4 days). However, for cod and haddock, the differences were larger. In the case of cod, the peak of the spawning season was nearly one month later in the mid area, compared to the southern area (8<sup>th</sup> of March against 5<sup>th</sup> of April), while the difference between the mid and north areas was only four days. Haddock showed a more distinct difference in the peak of the spawning season across all areas.

The difference from the south to the mid area was about 21 days (30<sup>th</sup> of March to 22<sup>nd</sup> of April), and the difference from the mid to the northern area was 24 days (22<sup>nd</sup> of April to 16<sup>th</sup> of May).

The spawning peak for cod and saithe occurred before day 120 in all areas, while for haddock, this only occurred in the southern and mid areas. In the mid area, the spawning peak happened nine days before day 120, while in the northern area, it occurred 15 days after day 120.



**Figure 3.3:** Visually comparing the fitted values from the GLM model across the three different species: cod (green), haddock (brown), and saithe (yellow). The comparison takes place in the North, Mid and South areas. The date represents the day with the maximum probability of an individual of each species to be a spawner within the respective areas. Day number 120 marks the official end of sampling the maturation stages in the Norwegian Reference Fleet.

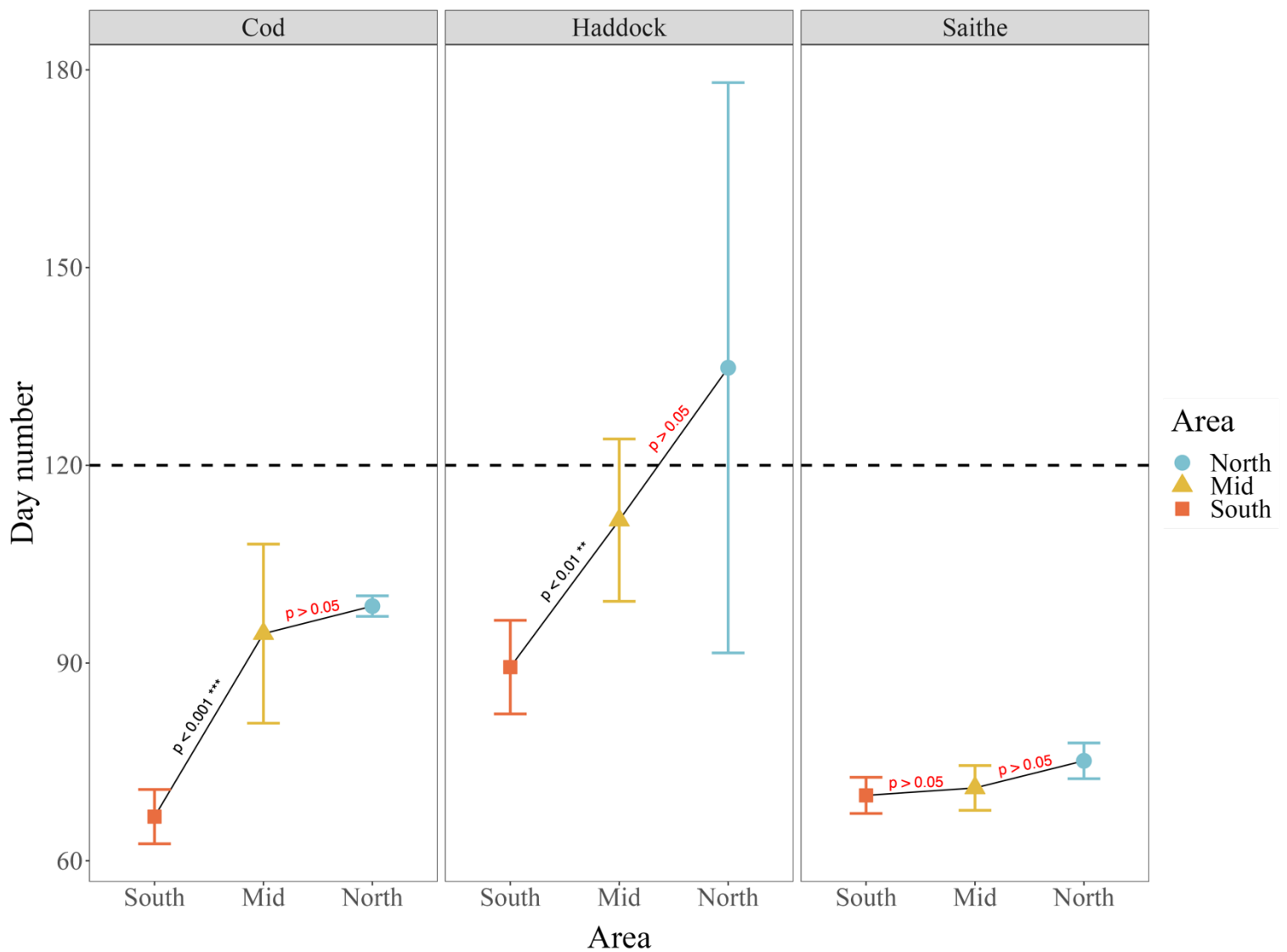
**Table 3.1:** Day number corresponding to the maximum probability of observing a spawning individual for the different species: cod, haddock, and saithe and at different areas: North, Mid and South. The estimated standard error was derived from delta method using the output of the full GLM model. Additionally, the day number is represented by the specific date.

AREA	COD			HADDOCK			SAITHE		
	Day number	SE	Date	Day number	SE	Date	Day number	SE	Date
North	98.6	0.8	9 <sup>th</sup> April	135	22.1	15 <sup>th</sup> May	75.2	1.4	16 <sup>th</sup> March
Mid	94.5	6.9	5 <sup>th</sup> April	111.7	17.8	22 <sup>nd</sup> April	71	1.7	12 <sup>th</sup> March
South	66.7	2.1	8 <sup>th</sup> March	89.4	3.6	30 <sup>th</sup> March	69	1.4	10 <sup>th</sup> March

For cod and haddock, there was a significant difference between the estimated peak of the spawning season between the south and mid area (cod:  $p < 0.001$ , haddock:  $p < 0.01$ ) (Figure 3.4; Appendix B.2). However, despite having different estimated peak dates, there was no significant difference between the mid and northern areas for either species ( $p > 0.05$ ).

The timing of the spawning peak had large uncertainty for haddock in the mid and especially in the north area, which was also observed for cod in the mid area. Regarding saithe, there was no significant difference ( $p > 0.05$ ) in the timing of the spawning peak between the south and mid area or the mid and northern area.

All three species showed a significant difference in the timing of the spawning peak between the southern and northern areas (cod:  $p < 0.001$ , haddock:  $p < 0.05$ , saithe:  $p < 0.01$ ), indicating a geographical gradient in the timing of the spawning peak for all three species.

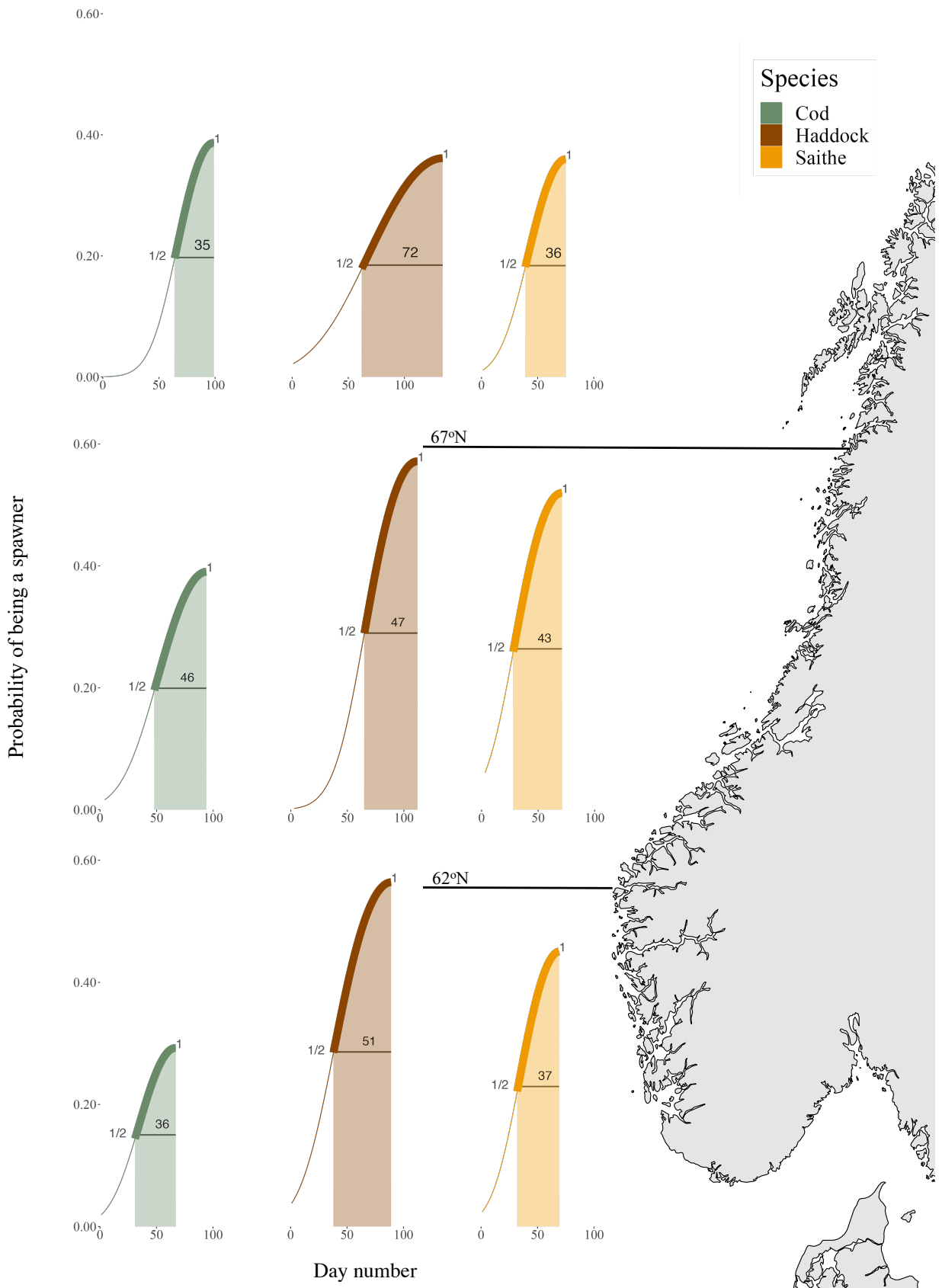


**Figure 3.4:** The day number of which cod, haddock and saithe have the highest probability to be a spawner within the three areas: North (blue), Mid (yellow), and South (red). These days were determined using the delta method, applied to the output from the full GLM, also giving an estimate of the associated confidence interval (estimate  $\pm 1.96 * SE$ ). P-values represent the significant level between the estimated peaks between areas, where significant p-values are shown in black, while red represents non-significant p-values.

### 3.4 Duration of the spawning season

In terms of the duration of the spawning season, similar durations were observed for cod and saithe, with haddock having an overall longer spawning season (Figure 3.5). The results indicate that the duration of this period lasted between 35 to 72 days, with haddock exhibiting the longest duration and cod the shortest.

In the south area, cod had the shortest duration, with only 35 days, followed by saithe with 36 days and haddock having a duration of 51 days. In the mid area, both cod and saithe had their longest durations, among all areas, with 46 and 43 days, respectively. Haddock had a duration of 47 days. In the north area, haddock exhibited the longest duration of 72 days, while cod and saithe had a duration of 35 and 36 days.



**Figure 3.5:** The estimated duration of the spawning season for cod (green), haddock (brown) and saithe (yellow). The plot represents the fitted values from the full GLM model and shows the probability of being a spawner on different days since the 1<sup>st</sup> of January. The horizontal line represents the duration from when the probability of being a spawner is at its maximum (1) to when it is at its half of the maximum (1/2). The number of days between these two points is provided as a numerical value.

## 4 DISCUSSION

The purpose of this study was fourfold: (1) to assess the congruity between the spawning location data used in this master thesis and the existing spawning maps, (2) to examine differences in the timing of spawning among cod, saithe, and haddock, (3) to explore potential variations in the timing of spawning across a south-north gradient and (4) to explore the duration of the spawning season for cod, haddock, and saithe across the different areas

My results revealed that the current spawning maps do not provide adequate coverage for the spawning areas in the northern region of Norway for either of the three species. Additionally, my investigation demonstrated distinct differences in the timing of spawning among the three species, with saithe spawning earliest, followed by cod and haddock. These species also displayed a south-north gradient in their timing of spawning, with a significant difference between the south and north area for all three species. Furthermore, the results indicated a contrasting duration of the spawning season among the species, with cod and saithe having a shorter spawning duration compared to haddock.

In this discussion, I will summaries and compare my findings to prior research, interpret their implications within the realm of fisheries biology, and acknowledge the limitations of this study.

### 4.1 Spawning distribution

The results of this study demonstrate that the current maps used for management purposes do not provide complete coverage of the spawning areas for cod, saithe, and haddock. In the northern region, evidence points towards a northward shift of the spawning distribution for these species. These findings align with prior research, which has noted a north and eastwards variation in the positioning of spawning grounds for both NEA cod (Sundby & Nakken, 2008, Opdal, 2010) and NEA haddock (Landa et al., 2014; Langangen et al., 2018). Such shifts have been attributed to the cost associated with spawning migrations, with the exact mechanisms differing. For instance, a northward shift could potentially stem from an expansion of feeding grounds due to warmer temperatures (Kjesbu et al., 2014). Expanding feeding grounds northeastwards in the Barents Sea could thereby lead to spawning grounds further northeast, as migrations to more southern and previously known spawning grounds from the newly established feeding grounds become too long and costly (Sundby & Nakken, 2008).



The higher migration cost for smaller fish, compared to larger ones, might be a significant factor driving the observed northwards trend in spawning grounds (Jørgensen et al., 2008). This is particularly relevant considering the demographic and phenotypic changes caused by the selective harvesting of fish populations (Pauli & Heino, 2014). Over time, this can alter the age and length composition of the population, leading to a decreased age diversity and earlier maturation (Pauli & Heino, 2014; Enberg et al., 2009; Heino et al., 2015). Given that smaller fish to a less extent degree benefit from such long migrations, there is likely that the number of individuals conducting spawning migrations to more southernly spawning grounds could decrease as these areas become too distant from the feeding grounds (Jørgensen et al., 2008).

A northward shift in the spawning grounds has also been correlated with the spawning stock biomass (SSB) (Langangen et al., 2018). Langangen et al. (2018) found that years with high SSB resulted in a more northern spawning ground, implying a density-dependent mechanism affecting the northward shift. Landa et al. (2014) found that high temperatures were followed by high biomass for the Northeast Arctic haddock but that year-to-year variations in the northward's distribution are more related to the stock abundance. Johannesen et al. (2020) also suggested that the Northeast Arctic cod expanded their feeding ground further north when the stock increased.

## 4.2 Peak of the spawning season

My results confirmed my predictions of a significant geographical gradient in the peak spawning time for cod, haddock, and saithe along a south–north gradient. All species experienced the earliest peak in the spawning season in the south area, followed by the mid and the last peak in the north area. Consequently, the North Sea stocks of cod, haddock and saithe appear to reach their spawning peak earlier than the Northeast Arctic stocks. This pattern seems to follow the onset of the spring bloom, which follows a similar pattern from low to higher latitudes in the northern hemisphere (Racault et al., 2012).

It is reasonable to assume that this temporal pattern might represent a strategic adaptation to optimize feeding conditions for the larvae during their critical period (Cushing, 1990). Any failure to this match could lead to recruitment failure (Houde, 2016). Prior research by Ferreira et al. (2020) demonstrated that recruitment variability could be explained by the overlap between larvae and prey, underscoring the critical role of timing for survival and reproduction

success. Considering the potential of missing this peak period of prey availability, it can be reasonable to believe that the timing of the spawning has evolved to align with the spring bloom.

The initiation of the spring bloom system in the northern hemisphere is largely dependent on light availability, as Sommer & Lengfellner (2008) pointed out. However, one sees annual fluctuations in the onset of the spring bloom, as demonstrated by Dalpadado et al. (2020) in the Barents Sea. This variability can be attributed to the different mechanisms required for a spring bloom to occur, such as the water column stratification.

The regulatory role of light seems also to extend beyond the spring bloom initiation, as several studies have identified the importance of light during the spawning season. Research conducted by Hansen et al. (2001), Skjæraasen et al. (2004), and Martin-Robichaud & Berlinsky (2004) provided compelling evidence that altering the photoperiod could have a significant impact on the timing of maturation and spawning in Atlantic cod and haddock. Moreover, Otterå et al. (2006) found that captive coastal cod from various sites along the Norwegian coast displayed different spawning times, even though they were maintained in the same environment. The findings suggest that cod populations in different regions may have evolved distinct adaptations to local light cues, using these as triggers for the onset of their spawning season. These external cues can be used to enhance the chance of gonad development and spawning taking place at a suitable time, enabling spawning to occur at a time when the conditions are sufficient for offspring survival.

Cod larvae start their external feeding around 14 days after hatching, depending on their surrounding temperature (Hall et al., 2004). During this period, the cod larvae consume plankton from several trophic levels (Van der Meeren, 1991). If this feeding pattern also applies to saithe, it may suggest that saithe, to a greater degree, consume phytoplankton during the early spring bloom, while cod and haddock may rely on the zooplankton prey, which becomes more abundant later in the season.

Given that phytoplankton is a nutrient-rich source, enhancing the growth and survival of fish larvae in aquaculture (Napiórkowska-Krzebietke, 2017), it may be a preferred food source for saithe larvae. This preference could explain why saithe spawn earlier than cod and haddock, but not why the exact timing of spawning is consistent across different regions. The consistency of the spawning event for saithe fuels for speculations, and it would be interesting to investigate

if the onset of the spawning season was associated with the lunar cycle, a phenomenon that fishermen have reported.

Interestingly, the recruitment of saithe is the most stable among these three species, followed by cod and haddock having the greatest variations (Dolgov et al., 2013; ICES 2021; Johannesen et al., 2022). This pattern might suggest that an early onset of the spawning season could lead to more consistent recruitments. On the other hand, late spawning could carry a potential risk of missing the spring bloom peak, which could lead to lack of food sources for the larvae and thereby leading to lower recruitment levels. However, if the timing of the spring bloom aligns with their spawning period, it could result in higher recruitment rates.

### 4.3 Duration of the spawning season

In this study, I investigated the length of the spawning season for cod, saithe, and haddock to explore the existence of a south–north gradient. I hypothesized that the spawning season might be extended in the northern region due to interannual variations in the spring bloom system (Dalpadado et al., 2014) as an adaptation to an enhanced likelihood of spawning at a time so the larvae can feed on the plankton peak.

Contrary to expectations, my finding provided no evidence of a south–north gradient in the length of the spawning season. Instead, all the species exhibited the longest spawning season in the mid area, except for haddock, which showed the longest spawning duration in the north area. Various factors can potentially influence the duration of the spawning season. One such factor could be the number of egg batches released during the spawning season and the time interval between these releases. Hislop et al. (1978) found that haddock typically release 16.6 batches of eggs over approximately 33 days, with a time interval between 24 to 48 hours. Cod showed a spawning season lasting for about 50 – 60 days, with 17 – 19 batches, where the time interval between the batches was highly diverse (Kjesbu, 1989). This, however, contradicts my findings, as haddock had a longer spawning season in all areas compared to cod in my study.

The results of my study may be influenced by the existence of distinct subpopulations in various regions along the Norwegian coast. According to Dahle et al. (2018b), genetic analysis of coastal cod revealed genetic variations along the Norwegian coast. This implies that these populations often remain within geographical regions and have limited migration over large

distances (Dahle et al., 2018b). The peak and length of the spawning season may vary between the different subpopulations, thereby causing the average spawning period to appear longer.

Berg et al., (2021) conducted a genetic study of Atlantic haddock and discovered a potential barrier at Lofoten Island, Individuals situated outside Lofoten were more genetically similar to those individuals located further north, while the individuals in Vestfjorden were more genetically similar to those located further south (Berg et al., 2021). Castaño-Primo et al. (2014) observed that eggs and larvae from haddock spawning in Vestfjorden did not drift towards the Barents Sea, unlike those from other areas such as outside of Lofoten and Tromsøflaket. Similar observations were made by Myksvoll et al. (2014) regarding Atlantic cod eggs, where eggs released in oceanic areas were transported northwards along the Norwegian Coast, while eggs spawned in fjords had a higher retention rate. This could indicate a genetic break around the Lofoten area, potentially influencing the timing and genetic structure of individuals spawning inside and outside the Lofoten Islands. Consequently, Berg et al. (2021) speculated that haddock spawning inside Vestfjorden might be more coastal bound as the retention rate is higher, while those spawning outside could be more migratory individuals. As for saithe, Myskvoll et al. (2021) found that the population in the central Northeast Atlantic is well-connected and distributed over several management units, which could explain the similarities in the spawning times for saithe in the South, Mid and North areas.

#### 4.4 Limitations

##### **Method used**

Studying spawning events is important for scientific and management purposes as it provides critical information for understanding the biology and ecology of fish populations necessary for sustainable management. Various methods have been employed over time to investigate these events, including the estimates of egg production during egg surveys (Sundby & Solemdal, 1984) and the Roe Index (RI), a relationship between the roe weight in the landed catch divided by the weight of the female in the catch (Pedersen, 1984).

In this thesis, I used data where the maturation stages are macroscopically determined. Determining the maturation stage macroscopically is often difficult, particularly during transitional stages, which can lead to inaccuracies in the data. As stage 3 indicates a spawning individual, it should be noted that this stage means that clear eggs are present in the gonad and

do not necessarily mean that the individual is actively spawning. Fish can carry these eggs for some time before releasing them, which may lead to a source of error when estimating the exact spawning time and give the impression of a wider extent of the spawning area.

### **Statistical analysis**

Regarding the statistical analysis, I assumed that the probability of being a spawning individual would follow a bell-shaped curve over time. However, this may not be entirely accurate due to unpredictable factors, such as the possible existence of distinct populations that may spawn at different times, and thereby influencing the shape of the curve.

An example of this could be the appearance of spawning individuals early in the season. By incorporating a quadratic term, the bell-shape curve will widen, as it assumes the first increase of spawning individuals to be the beginning of the spawning season. By identifying different populations, which may exhibit different spawning activities, one could get a better indication of how the spawning season might be.

According to the guidelines of the Reference Fleet, they should end their sampling of maturation stages after day 120, while the Sampling Boat continues past this date. The Sampling Boat primarily collects data from the coastal fleet, in contrast to the reference fleet, which collects data from both coastal fleet and the high sea fleet. Therefore, the number of individuals found in the coastal areas is expected to be higher than in the high seas after day 120. The variation in data collection methods could potentially influence the observed timing and location of spawning reported in this thesis, if there in fact is a difference in the spawning season between individuals residing closer to the coast and those inhabiting the oceanic areas.

### **The use of fishery-dependent and fishery-independent data**

In this study, both fishery-dependent and fishery-independent data were utilized to provide a comprehensive analysis of the spawning season of the targeted fish species. While fishery-dependent data can be valuable for understanding fish populations and their dynamics, it is subject to limitations such as bias towards fishing in specific areas or at specific times. This can lead to an inaccurate representation of the true population, thereby limiting the accuracy of the data.

However, by using the fishery-dependent data sources in this study, I was able to achieve extensive coverage of the spawning season, which the fishery-independent data alone could not cover or provide insight into. Therefore, using both data sources in this study allowed for a more complete understanding of the spawning season of cod, haddock, and saithe.

## **5 CONCLUSIONS**

In conclusion, the present study has provided valuable insight into the spawning event of cod, haddock, and saithe. By examining the spawning area, the spawning season's peak, and the spawning season's duration, we have shed light on the lacking coverage in the spawning maps of areas in the northern region and a south-north gradient of the peak of the spawning season for cod, haddock, and saithe.

While this study has some limitations, including a limited temporal and spatial coverage of fishery-independent data, and challenges in determining maturation stages, this study aims to offer valuable insights in the field of fishery biology and management. I hope this work will inspire further research in this field to better understand the complex spawning phenology of these species and to be able to implement these findings into management.

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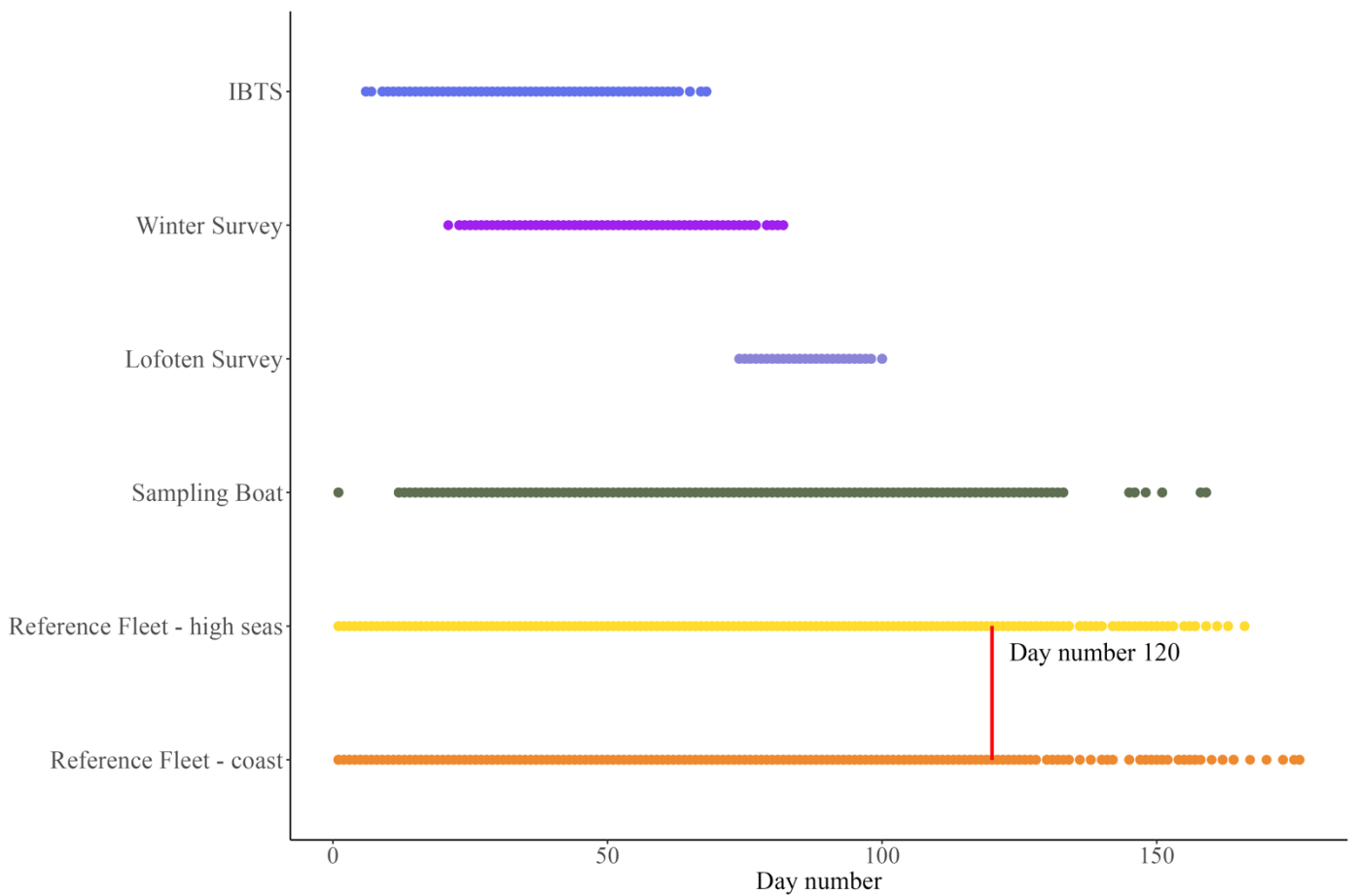
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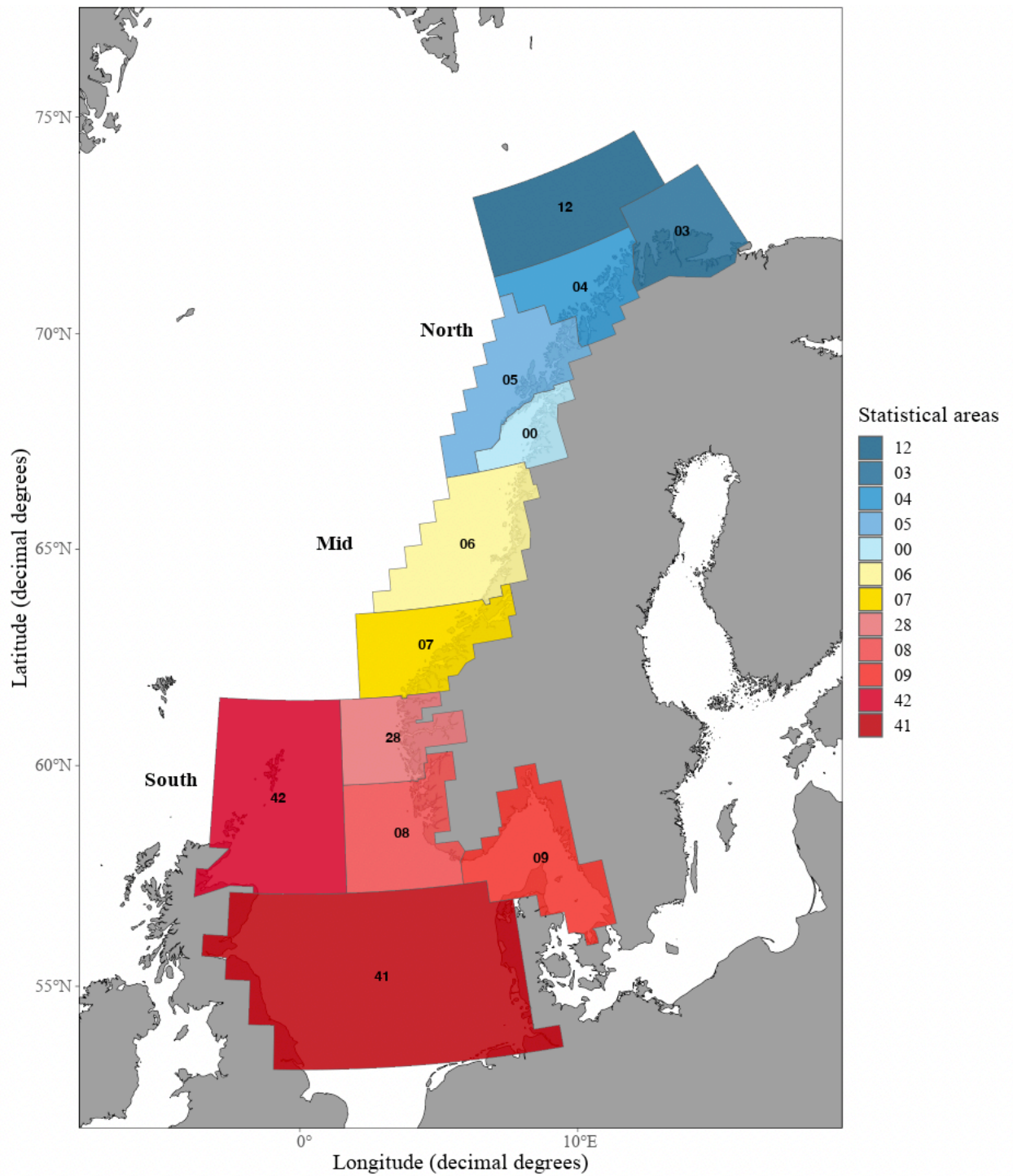
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## APPENDIX A



**Appendix A.1:** Illustration of the sampling duration of mature female individuals (maturation stage 2, 3 or 4) from various platforms throughout the thesis focus time (January - June). The platforms include is the IBTS, the Winter Survey, the Lofoten Survey, the Sampling Boat, the Reference Fleet – high seas, and the Reference Fleet – coastal. Each point corresponds to a unique day of data collection.



**Appendix A.2:** The study area for this master thesis, highlighting three distinct regions used for statistical analysis: North, Mid and South. The North area includes the statistical areas 12, 03, 04, 05, and 00, represented by blue shades. Mid area includes the statistical areas 06 and 07, represented by yellow shades. The South area includes the statistical areas 28, 08, 09, 41, and 42, represented as red shades.

**Appendix A.3:** The number of individuals sampled from different sampling platforms (IBTS, Winter Survey, Lofoten Survey, the Sampling Boat, the Ference Fleet – high seas and the Reference Fleet – coast) across the different areas (North, Mid and South). The count provided represents the number of female individuals with maturation stages 2, 3 and 4, that were sampled from the different platforms in the specific area.

AREA	IBTS	WINTER SURVEY	LOFOTEN SURVEY	SAMPLING BOAT	REFERENCE FLEET	
					HIGH SEAS	COAST
North	0	3 511	5 936	29 931	14 207	12 585
Mid	0	0	0	1 071	5 718	5 365
South	17 951	0	0	0	3 775	5 818
<b>Total</b>	<b>17 951</b>	<b>3 511</b>	<b>5 936</b>	<b>31 002</b>	<b>23 700</b>	<b>23 768</b>

*Appendix A.4:* The R packages utilized in this master’s thesis and their respective references.

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R PACKAGE	REFERENCE
dplyr	Wickham, H., François, R., Henry, L., Müller, K., & Vaughan, D. (2023). dplyr: A Grammar of Data Manipulation. Retrieved from <a href="https://dplyr.tidyverse.org">https://dplyr.tidyverse.org</a> and <a href="https://github.com/tidyverse/dplyr">https://github.com/tidyverse/dplyr</a>
ggoceanmap	Vihtakari, M. (2022). ggOceanMaps: Plot Data on Oceanographic Maps using 'ggplot2'. R package version 1.3.7, <a href="https://mikkovihtakari.github.io/ggOceanMaps/">https://mikkovihtakari.github.io/ggOceanMaps/</a>
ggplot2	Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. ISBN 978-3-319-24277-4. Retrieved from <a href="https://ggplot2.tidyverse.org">https://ggplot2.tidyverse.org</a>
marginaleffects	Arel-Bundock, V. (2023). <i>marginaleffects: Predictions, Comparisons, Slopes, Marginal Means, and Hypothesis Tests</i> . R package version 0.12.0, <a href="https://vincentarelbundock.github.io/marginaleffects/">https://vincentarelbundock.github.io/marginaleffects/</a> .
mgcv	Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models.” <i>Journal of the Royal Statistical Society (B)</i> , 73(1), 3-36.
sf	Pebesma, E. (2018). “Simple Features for R: Standardized Support for Spatial Vector Data.” <i>The R Journal</i> , 10(1), 439–446. <a href="https://doi.org/10.32614/RJ-2018-009">https://doi.org/10.32614/RJ-2018-009</a> .
tidyr	Wickham, H., Vaughan, D., & Girlich, M. (2023). tidyr: Tidy Messy Data. Retrieved from <a href="https://tidyr.tidyverse.org">https://tidyr.tidyverse.org</a> and <a href="https://github.com/tidyverse/tidyr">https://github.com/tidyverse/tidyr</a>

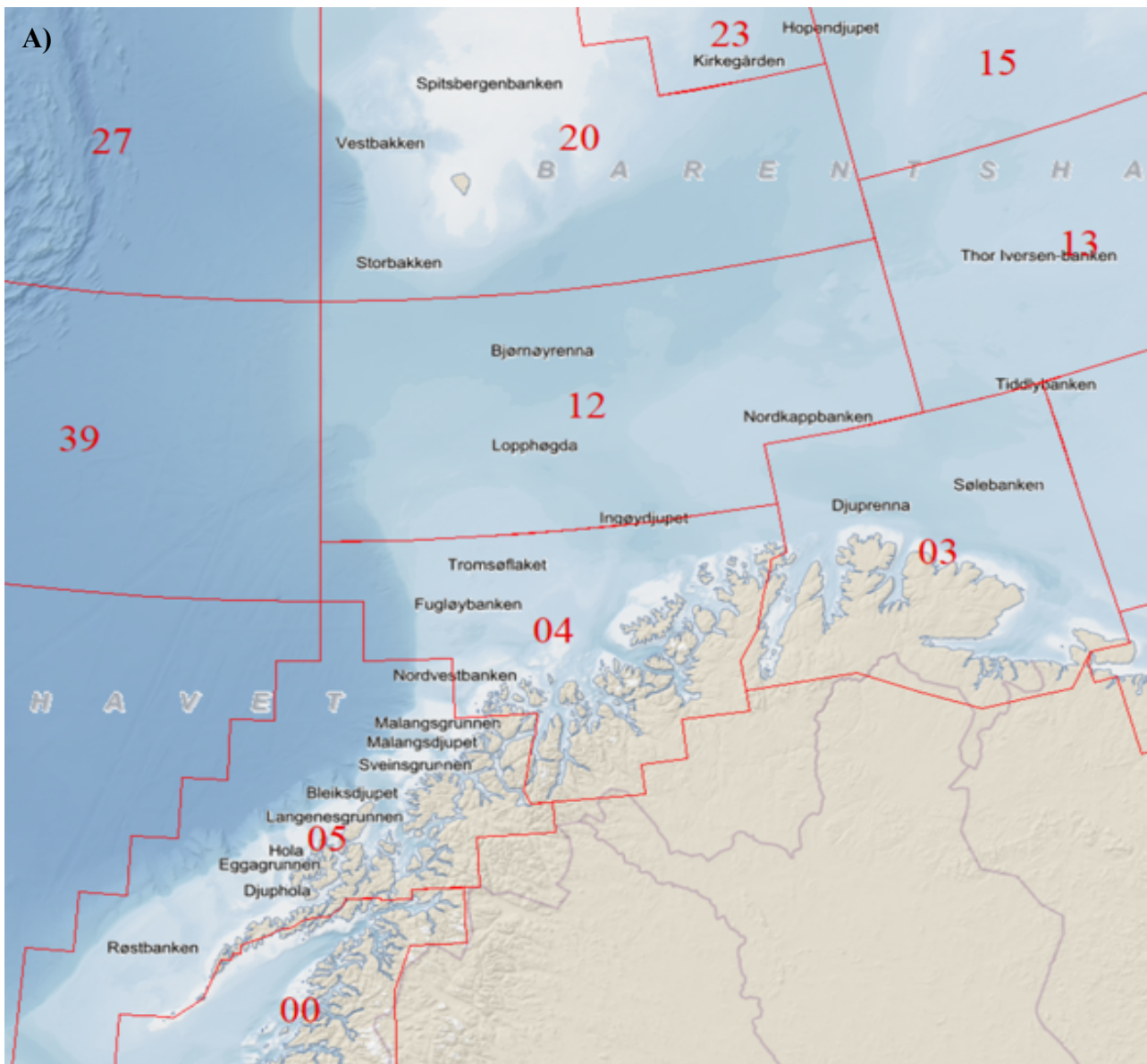
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**Appendix A.5:** Five different Generalized Linear Models (GLMs) with the Akaike Information Criterion (AIC) values, provided for each model and each species. In the statistical analysis, the model with the lowest AIC was selected (model 5).

MODEL	PREDICTOR VARIABLE	AIC		
		Cod	Haddock	Saithe
1	Day number	52809.63	37859.24	21685.78
2	Day number + Area	52668.88	36314.96	20895.65
3	Day number + Area + Day number:Area	52393.30	36236.74	20878.88
4	Day number + Day number <sup>2</sup> + Area	50758.52	35967.13	19652.02
<b>5</b> <b>Full model</b>	<b>Day number + Day number:Area + Day number<sup>2</sup> + Day number<sup>2</sup>:Area + Area</b>	<b>50012.92</b>	<b>35794.20</b>	<b>19629.99</b>

## APPENDIX B



*Appendix B.1:* Known fishing areas in northern Norway and in the Barents Sea. Edda Johannesen compiled this map in April 2023.

**Appendix B.2:** The estimated differences between two areas using the full model and the delta method. The estimated difference is the number of days between the estimated peak spawning days, along with the standard error (SE), the p-value and the confidence interval (estimate  $\pm$  1.96 \* SE).

SPECIES	AREA	ESTIMATED DIFFERENCE	SE	p-value	CONFIDENCE INTERVAL	
					Low	High
<b>Cod</b>	South - Mid	27.76	7.24	< 0.001 ***	13.56	41.96
	Mid - North	4.17	6.97	0.549	-9.49	17.85
	South - North	31.93	2.24	< 0.001 ***	27.53	36.34
<b>Haddock</b>	South - Mid	22.29	7.25	< 0.01 **	8.08	36.51
	Mid - North	23.11	22.94	0.313	-21.86	68.09
	South - North	45.41	22.36	< 0.05 *	1.57	89.25
<b>Saithe</b>	South - Mid	1.13	2.22	0.612	-3.24	5.50
	Mid - North	4.11	2.21	0.063	-0.23	8.45
	South - North	5.24	1.96	< 0.01 **	1.38	9.09